

## Chapter 2

## THE SOURCE OF ALGAL COLONIZERS ON ROCK SUBSTRATES IN A FRESHWATER IMPOUNDMENT.

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## ABSTRACT

The source of algal colonizers onto rock substrates in a eutrophic reservoir was analyzed during the spring diatom pulse by placing sediment traps in and beyond the periphyton growth zone and by scraping intact surfaces of known age. Impingement or "raining" of diatom cells from the water column was more important in the recolonization of rock surfaces than direct encroachment from the adjacent attached community. Relative to substrate-associated standing crops ( $\bar{x} = 2.16 \times 10^4$  cells  $\text{mm}^{-2}$ ), high densities of planktonic and periphytic diatoms impinged from the water column ( $\bar{x} = 5.03 \times 10^3$  cells  $\text{mm}^{-2} \text{d}^{-1}$ ), particularly in the upper (surge) zone. Direct encroachment from immediately adjacent populations contributed very little quantitatively (none detected) or qualitatively (6 rare taxa of 67 total diatom taxa found) to the recolonization of denuded surfaces. Storm-induced turbulence reduced natural periphyton densities by up to 47%, with pseudoperiphytic species (e.g., *Fragilaria vaucheriae*) exhibiting greater losses than attached forms. The percentage of nonliving diatoms on rock substrates increased during calm periods, prior to storm events.

## 2.1 INTRODUCTION

Objects submerged in marine or fresh waters are readily colonized by microalgae and bacteria in a brief period of time. Bacteria colonize natural and artificial surfaces within a few hours (Gerchakov et al., 1976; Zachary et al., 1978; Fletcher, 1980; Dempsey, 1981), while diatoms and other microbes immigrate onto substrates within a day to several weeks (Cundell and Mitchell, 1977; Colwell et al., 1980; Hudon and Bourget, 1981; Hoagland et al., 1982). Diatoms and other microorganisms have also been shown to attach to a variety of substrates under laboratory or experimental field conditions (Rosemarin and Gelin, 1978; Marszalek et al., 1979; Tuchman and Stevenson, 1980; Blinn et al., 1980), including surfaces coated with toxic paints (Callow et al., 1976; Callow and Evans, 1981; Daniel and Chamberlain, 1981). Rapid colonization occurs not only on inshore rocks, pilings, aquatic vegetation, etc., but also in open water on oil platforms, ship hulls, and buoys (Evans, 1981; Characklis and Cooksey, 1983; Terry and Edyvean, 1984; Roemer et al., 1984).

Despite the universality of the colonization or fouling phenomenon, very little is known about the source of microalgal immigrants onto marine or fresh-water substrates. Structures located in the pelagic zone are presumably colonized by tychoplanktonic species which comprise a low proportion of the pelagic assemblage, although this assumption awaits testing. Periphytic algae immigrating onto substrates in the littoral zone potentially emigrate from a number of sources, including the water column, adjacent surfaces, sand and sediments in deeper water, etc. Brown and Austin (1973) demonstrated an exchange of cells between the phytoplankton and periphyton (attached algae), particularly following fall turnover. As the planktonic diatom Fragilaria crotonensis settled out of open water, it appeared on artificial substrates, constituting as much as forty percent or more of the periphyton relative abundance (perhaps a dying population, although viable cell numbers were not reported). Other studies have revealed a similar inverse relationship between free-floating and attached communities (Kairesalo, 1976; Moss, 1981; Oleksowicz, 1982).

Previous reports in our study reservoir have shown that portions of attached communities on rock substrates can peel or slough off under certain conditions (Roemer et al., 1984). Similar findings have been reported for a variety of other aquatic habitats (Castenholz, 1961; King and Ball, 1966; Hoagland, 1983). The present study was designed to investigate the simple model illustrated in Fig. 1. We postulated that colonizers on denuded portions of substrates could emigrate from the community immediately surrounding the cleared area and/or impinge from the water column above. Direct encroachment would be attributable to motile diatoms associated with the substrate adjacent to the denuded area, whereas impingement could include periphytic or tychoplanktonic members regardless of their origin. The specific question that this study addressed was: what is the relative importance of these two principal sources to recolonization? Experimental field manipulations were conducted during the spring diatom growth pulse in an extensive epilithic community (attached to rock), to evaluate the contribution of each of these major sources.

## 2.2 MATERIALS AND METHODS

### 2.2.1 Study site

McConaughy reservoir is a large, eutrophic impoundment constructed for flood control, recreational use, and hydroelectric power generation (Table 1). The reservoir is located on the North Platte River in western Nebraska, U.S.A., near the foot of the Sandhills region in Keith County (T.14N, R.38,39W and T.15N, R.38-42W). Spring and autumn diatom blooms occur annually in the plankton and periphyton. Despite its productive trophic status, the deeper eastern end of the reservoir is relatively clear, allowing development of dense epilithic algal

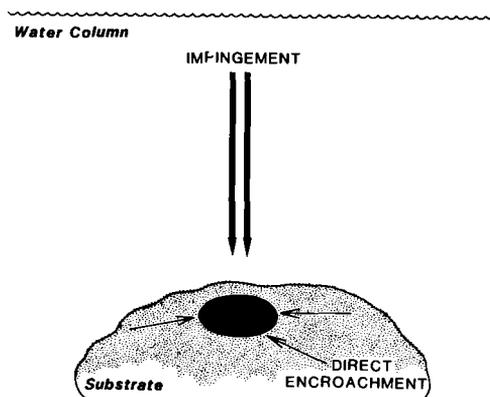


Fig. 2.1. Model for possible source(s) of immigrants in recolonization of denuded area of rock substrate (dark circle).

stands down to 6 m or more on the rocky dam. Quantum irradiance values, as well as additional morphometric, physical and chemical data have been published for this reservoir (Roemer and Hoagland, 1979). Due to the reservoir's basic east-west orientation, fetch, and the prevalence of W-SW winds during the growing season, the rocky dam is periodically subjected to severe wave action.

### 2.2.2 Field collections

Algal cells "raining" from the water column were collected using sediment traps, consisting of 21.2 cm lengths of 4.1 cm diameter PVC plastic tubes, darkened on the inner surface to reduce light reflection. The height:diameter ratio of ca. 5, the wide spacing between tubes (34 cm) and between the tubes and the center support pole (35 cm), and the simple tube design, follow the design suggestions of Hargrave and Burns (1979) and reviews by Bloesch and Burns (1980) and Blomquist and Håkanson (1981). Tubes were occluded on one end with a rubber stopper to facilitate later removal of sedimented material. The center support and base were constructed from a PVC pipe anchored in a concrete block (combined tube and support height = 1.39 m). A sediment trap apparatus was located in 3 m of water (to top of trap), adjacent to rock substrates described below, and in 6.7 m of water, beyond the rock dam and beneath open water, ca. 25 m from the shallow trap. Based on underwater observations following storm events, storm-induced wave action does not translate to the lower depth. All traps were placed in the field on 22 June 1984. One tube was collected every 4d until 12 July 1984. On each sampling date, a new trap was also introduced and collected four days later, to provide 4d "instantaneous" information in addition to the cumulative trap data. All samples were collected with the aid of SCUBA by stoppering the open upper end of the trap, returning it to the boat, and placing

TABLE 2.1

Selected physico-chemical properties of McConaughy reservoir.

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Maximum depth (m)	50.0
Mean depth (m)	16.9
Maximum length (km)	35.0
Maximum width (km)	5.6
Volume ( $\times 10^6$ m <sup>3</sup> )	2,400.0
Surface area (hectares)	14,164.0
Alkalinity (mg/l CaCO <sub>3</sub> )*	176.0
Silica (mg/l)*	24.0
pH*	8.6

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\*mean values, from Roemer and Hoagland (1979).

it in an ice chest for transport to the lab. Traps were then emptied, rinsed, and the sedimented material was fixed with 6:3:1 (water:ethanol:formalin) preservative (Prescott, 1970).

The relative contribution of direct encroachment to recolonization was tested by brushing clean pairs of circular areas (9 cm in diameter) on large horizontal rock surfaces along the face of the dam. A PVC ring (8.8 cm dia., 1.8 cm height) was cemented around one of each pair using marine epoxy putty (Permalite Plastics Corp., Newport Beach, CA) to prevent direct encroachment from the periphyton surrounding the denuded area. Three replicate pairs of ringed and unringed samples were collected every 4d concurrent with sediment trap samples, using a modified syringe apparatus similar to that described by Loeb (1981). In addition, semi-quantitative samples were taken from three nearby areas of unscraped rock, by brushing material from similar areas (with respect to location and surface area) into a plastic collection jar. All samples were taken using SCUBA and fixed in the field with 6:3:1.

### 2.2.3 Laboratory methods

All sediment trap and epilithic samples were divided into two equal portions; one portion was boiled in concentrated HCl for ca. 2 hr. to remove all organic matter. After several rinses with distilled water, a measured portion of the concentrate was air dried onto a 22 mm<sup>2</sup> coverslip and permanently mounted in Hyrax. A total of 500 diatom valves were counted from each slide using an Olympus microscope equipped with a 100X planachromat objective (N.A.=1.30).

The remaining portion of each fixed sample was used for nondiatom algae counts and to determine the percentage of living versus nonliving diatom cells (by the presence or absence of intact chloroplasts). Nondiatom algae were tabulated from 30 random Whipple fields at 200X from each of two Sedgewick-Rafter cells. McAlice (1971) indicated that counting 30 random fields yields

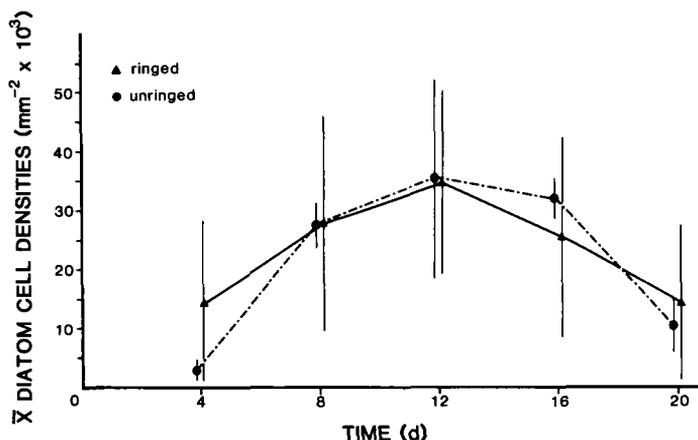


Fig. 2.2. Mean diatom cell densities ( $\text{mm}^{-2} \times 10^3$ ) on ringed and unringed rock substrates.  $P \gg 0.05$ ;  $n = 30 \pm 1$  SD.

90-95% of all species present. Approximately 100 cells of the dominant diatom genera were counted from a total of three Whipple fields at 400X using a Palmer cell. If 100 cells of a given genus were encountered before three fields were scanned, counts were continued until three fields had been completed.

Diatom habitat preferences were based principally on information contained in Lowe (1974), Patrick and Reimer (1966; 1975), Beaver (1981), and on direct observations of growth habits.

## 2.3 RESULTS

Eighty-four diatom taxa representing 21 genera were found among the 31,500 valves tabulated from 63 samples. In addition, 24 nondiatom algae were identified from preserved samples. The substrate occurrences of each taxon, its habitat preference (excluding nondiatom algae), and the total number of taxa found in each collection type are listed in Table 2. The most abundant taxa encountered were Fragilaria vaucheriae, Achnanthes minutissima, Cymbella affinis, F. crotonensis, and Asterionella formosa. A total of 16 diatom taxa were unique to sediment trap (10 unique taxa), ringed (3), unringed (2), or unscraped (1) rock samples.

### 2.3.1 Encroachment

Diatom cell densities from ringed and unringed substrates are illustrated in Fig. 2. The two curves coincided closely, as mean densities for both increased through day 12, then decreased until day 20. No statistically significant difference between the two populations of means was detected (t-test;  $p \gg 0.05$ ,

TABLE 2.2

Occurrences of algal taxa by sample type (based on its presence in at least one sample) and the growth habit of each diatom taxa. ST=sediment trap, RG=ringed rock, URG=unringed rock, RK=unscraped rock.

BACILLARIOPHYCEAE	ST	RG	URG	RK	Growth Habit <sup>1</sup>
<b>CENTRICS</b>					
<u>Aulacosira ambigua</u> (Grun.) Simonsen	X	X	X	X	PL
<u>Cyclotella atomus</u> Hust.	X	X			PL <sup>2</sup>
<u>C. stelligera</u> P.T. Cl. ex Grun.	X	X	X	X	P
<u>M. granulata</u> (Ehr.) Ralfs	X	X	X	X	PL
<u>M. granulata</u> var. <u>angustissima</u> Müll.	X	X	X	X	PL
<u>M. varians</u> Ag.	X	X	X	X	P
<u>Stephanodiscus minutula</u> (Kütz.)Round	X	X	X	X	PL
<b>PENNATES</b>					
<u>Achnanthes deflexa</u> Reim.	X	X	X	X	(P)
<u>A. linearis</u> (Wm. Smith) Grun.	X				(P)
<u>A. minutissima</u> Kütz	X	X	X	X	P
<u>Amphora ovalis</u> var. <u>pediculus</u> (Kütz.) Grun.	X	X	X	X	P
<u>A. perpusilla</u> (Grun.)Grun.	X	X	X	X	(P)
<u>A. veneta</u> Kütz.	X				P
<u>Asterionella formosa</u> Hass.	X	X	X	X	PL
<u>Caloneis bacillum</u> (Grun.) Cl.	X	X	X	X	P
<u>Cocconeis diminuta</u> Pant.	X				P
<u>C. pediculus</u> Ehr.	X	X	X		P
<u>C. placentula</u> var. <u>euglypta</u> (Ehr.)Cl.		X			P
<u>Cymatopleura solea</u> (Bréb.)Wm. Smith	X	X	X	X	P
<u>Cymbella affinis</u> Kütz.	X	X	X	X	P
<u>C. amphicephala</u> Naeg.	X	X		X	P
<u>C. cesatii</u> (Rabh.)Grun.	X				P
<u>C. cistula</u> (Ehr.)Kirchn.	X	X	X	X	P
<u>C. cymbiformis</u> Ag.		X	X		P
<u>C. laevis</u> Naeg. ex Kütz.	X	X	X	X	P
<u>C. mexicana</u> (Ehr.)Cl.	X	X	X	X	P
<u>C. microcephala</u> Grun.	X	X	X	X	P
<u>C. minuta</u> Hilse ex Rabh.	X	X	X	X	P
<u>C. muelleri</u> Hust.	X	X	X	X	
<u>Denticula elegans</u> Kütz.	X	X	X	X	P
<u>Diatoma tenue</u> var. <u>elongatum</u> Lyngb.	X	X	X	X	
<u>D. vulgare</u> Bory	X	X	X	X	P
<u>Diploneis pseudovalis</u> Hust.				X	(P)
<u>Fragilaria brevistriata</u> (Grun.) Hust.			X	X	P
<u>F. brevistriata</u> var. <u>inflata</u> (Pant.)	X	X	X	X	(P)
<u>F. capucina</u> Desm.		X			P
<u>F. capucina</u> var. <u>mesolepta</u> Rabh.	X	X	X		(PL)
<u>F. construens</u> (Ehr.)Grun.	X	X	X	X	P
<u>F. crotonensis</u> Kitton	X	X	X	X	PL
<u>F. pinnata</u> Ehr.	X	X	X	X	P
<u>F. vaucheriae</u> (Ehr.) Petersen	X	X	X	X	(PL) <sup>3</sup>
<u>Gomphoneis erienne</u> (Grun)Skv. & Meyer	X			X	P
<u>G. herculeana</u> var. <u>robusta</u> (Grun.)Cl.?	X				P

	ST	RG	URG	RK	Growth Habit <sup>1</sup>
<u>Gomphonema accuminatum</u> Ehr.	X				P
<u>G. intricatum</u> Kütz.		X	X		P
<u>G. olivaceum</u> (Lyngb.)Kütz.	X	X	X	X	P
<u>G. parvulum</u> (Kütz.)Grun.	X				P
<u>G. truncatum</u> Ehr.	X				P
<u>Navicula arvensis</u> Hust.		X			(P)
<u>N. biconica</u> Patr.	X	X	X	X	(P)
<u>N. capitata</u> Ehr.	X				P
<u>N. capitata</u> var. <u>hungarica</u> (Grun.)Ross	X			X	P
<u>N. cryptocephala</u> Kütz.	X		X	X	(P)
<u>N. decussis</u> Østrup	X	X	X	X	
<u>N. menisculus</u> var. <u>upsaliensis</u> (Grun.) Grun.	X	X	X	X	(P)
<u>N. minima</u> Grun.		X	X		P
<u>N. mutica</u> Kütz.			X		PL
<u>N. mutica</u> var. <u>cohnii</u> (Hilse)Grun.	X				PL
<u>N. pupula</u> Kütz.	X				P
<u>N. radiosa</u> var. <u>tenella</u> (Bréb. ex Kütz.)Grun.	X	X	X	X	P
<u>N. reinhardtii</u> (Grun.)Grun.			X		
<u>N. salinarum</u> var. <u>intermedia</u> (Grun.)Cl.	X	X	X	X	(P)
<u>N. tripunctata</u> (O.F. Müll.)Bory	X	X	X	X	P
<u>Nitzschia acicularioides</u> Hust.	X				PL <sup>4</sup>
<u>N. amphibia</u> Grun.	X	X	X	X	p <sup>2</sup>
<u>N. angustata</u> (Wm. Smith)Grun.	X			X	(P)
<u>N. apiculata</u> (Greg.)Grun.	X		X	X	(P)
<u>N. denticula</u> Grun.	X	X	X	X	(P)
<u>N. dissipata</u> (Kütz.)Grun.	X	X	X	X	P
<u>N. fonticola</u> Grun.	X	X	X	X	P
<u>N. frustulum</u> Kütz.	X	X	X	X	P
<u>N. linearis</u> Wm. Smith	X	X	X	X	P
<u>N. microcephala</u> Grun.	X	X	X	X	P
<u>N. palea</u> (Kütz.) Wm. Smith	X	X	X	X	P
<u>N. sigmoidea</u> (Ehr.) Wm. Smith	X	X		X	P
<u>Rhoicosphenia curvata</u> (Kütz.)Grun.	X	X	X	X	P
<u>Surirella ovata</u> Kütz.		X	X		(P)
<u>S. angustata</u> Kütz.		X			
<u>Synedra acus</u> Kütz.	X	X	X	X	P
<u>S. filiformis</u> var. <u>exilis</u> Cl.	X	X	X	X	P
<u>S. radians</u> Kütz.	X	X	X	X	PL
<u>S. rumpens</u> var. <u>familiaris</u> (Kütz.)Hust.	X	X	X	X	P
<u>S. socia</u> Wallace			X	X	(P)
<u>S. ulna</u> (Nitz.)Ehr.	X	X	X	X	PL
Total Taxa/Sample Type	70	61	50	51	
Total Unique Taxa	10	3	2	1	
Total Diatom Taxa	84				

## OTHER ALGAE

<u>Ankistrodesmus</u> sp.	X	X	X	X	
<u>Aphanocapsa</u> sp.			X	X	
<u>Closterium</u> sp.	X	X			
<u>Cosmarium</u> sp.	X	X	X	X	
<u>Glenodinium</u> sp.		X			
<u>Lyngbya</u> sp.	X				
<u>Merismopedia</u> sp.	X	X	X	X	
<u>Mougeotia</u> sp.	X	X	X	X	
<u>Oocystis</u> sp.	X	X	X	X	

	<u>ST</u>	<u>RG</u>	<u>URG</u>	<u>RK</u>
<u>Oscillatoria</u> sp.	X	X	X	X
<u>Pediastrum Boryanum</u> (Turp.)Menegh.	X	X	X	X
<u>P. duplex</u> Meyen	X		X	X
<u>P. integrum</u> Naeg.		X		X
<u>P. obtusum</u> Lucks	X			
<u>Phacotus</u> cf. <u>lendneri</u> Chod.	X	X	X	X
<u>Phacotus</u> sp.	X	X	X	X
<u>Phacus</u> sp.	X	X		
<u>Phormidium</u> sp.	X	X	X	X
<u>Scenedesmus falcatus</u> Chod.			X	X
<u>Scenedesmus</u> sp.	X	X	X	X
<u>Spirogyra</u> sp.	X	X	X	X
<u>Staurastrum</u> sp.	X	X	X	X
<u>Stigeoclonium</u> sp.			X	
<u>Trachelomonas</u> sp.	X	X	X	X
<u>Ulothrix</u> sp.	X	X		X
Total Nondiatom Taxa = 25				

<sup>1</sup>p = periphytic PL = planktonic ( ) = assigned growth habit

<sup>2</sup>Hustedt (1938)

<sup>3</sup>Occurred in long chains

<sup>4</sup>Hustedt (1959)

n=30). In these as well as all other samples, the nondiatom algae comprised less than 10% of the total cell density. Two species of Phacotus (Chlorophyceae) were the most frequently encountered of these algae.

The overall mean percentages of planktonic diatoms tabulated in ringed and unringed substrate samples were 48.2% and 45.0% respectively. A comparison of all cell count values upon which these percentages were based indicated that there was no significant difference between the two treatments (t-test;  $p > 0.05$ ,  $n=30$ ; Table 3).

Little qualitative difference was found between ringed and unringed samples. Of the 67 diatom taxa identified from these substrates (Table 2), 6 were found only in samples from ringed surfaces and 6 from unringed. All of these unique taxa were uncommon, many occurring as a single valve in just one count. The most abundant and only planktonic form of the 13 unique taxa was Fragilaria capucina, which occurred in three counts from ringed substrates, with a maximum of 442 cells  $\text{mm}^{-2}$  (4.8% of total) in one day 8 sample.

### 2.3.2 Impingement from water column

Based on 4d (instantaneous) sediment trap samples, daily impingement rates ranged from  $0.84 \times 10^3$  to  $8.80 \times 10^3$  cells  $\text{mm}^{-2} \text{d}^{-1}$  in the upper growth zone and  $0.46 \times 10^3$  to  $3.70 \times 10^3$  cells  $\text{mm}^{-2} \text{d}^{-1}$  in the lower zone (Table 4). Further analysis indicated that accumulation densities in the two growth zones were significantly different (t-test;  $p < 0.05$ ); additional direct observations using SCUBA showed a striking difference. The mean daily impingement rate in the

TABLE 2.3

Mean percent planktonic diatoms from ringed and unringed substrates<sup>1</sup>.

<u>Date</u>	<u>Ringed</u>	<u>Unringed</u>
6/26	49.3	51.5
6/30	60.2	52.2
7/1	37.1	40.3
7/8	50.3	41.8
7/12	44.0	39.3
$\bar{x}$	48.2	45.0
S (% basis)	13.8	8.6

<sup>1</sup>three replicates.

TABLE 2.4

Instantaneous (4d) sediment trap accumulation rates in the upper (U) and lower (L) zones from June 22-July 12, 1984.

<u>Date</u>	<u>Zone</u>	<u>Diatom Accumulation Rate (cells mm<sup>-2</sup> d<sup>-1</sup> x 10<sup>3</sup>)</u>
6/26	U	0.84
	L	0.46
6/30	U	3.85
	L	1.11
7/4	U	8.80
	L	1.22
7/8	U	5.28
	L	*
7/12	U	6.40
	L	3.70
$\bar{x}$		3.52
S		2.90

\*Not available

upper zone 4d traps, adjacent to rock substrates, was  $5.03 \times 10^3$  cells  $\text{mm}^{-2} \text{d}^{-1}$ . This value constituted 48.8% of day 20 densities from unringed rock surfaces (Fig. 2) and 23.3% of the overall mean unringed sample density ( $2.16 \times 10^4$  cells  $\text{mm}^{-2}$ ). The initial 4d sediment trap (26 June) density of  $3.36 \times 10^3$  diatom cells  $\text{mm}^{-2}$  was greater than the day 4 unringed density ( $2.90 \times 10^3$  cells  $\text{mm}^{-2}$ ) and 23.5% of the day 4 ringed density, all collected on the same date. Qualita-

TABLE 2.5

Percentage of nonliving diatom cells in ringed (RG), unringed (URG), and unscrapped rock (RK) samples. (mean of three replicates).

Date	% Nonliving Diatoms		
	RG	URG	RK
6/26 (4d)	22	26	26
6/30 (8d)	23	31	28
7/4 (12d)	25	23	25
7/8 (16d)	32	28	32
7/12(20d)	12	20	25

tively, only 13 of the 84 diatom taxa identified in all counts did not occur in sediment traps (including cumulative traps; see Table 2).

The results of living versus nonliving diatom cell counts are listed in Table 5. In addition, five 4d sediment trap samples were selected at random and counted for comparative purposes. The percentage of nonliving diatom cells in these counts ranged from 18-34% ( $\bar{x}=26\%$ ). Comparison of these values with those from ringed, unringed, and unscrapped rock samples revealed no significant difference (t-test;  $p>0.05$ ,  $n=50$ ).

Diatom cell densities from cumulative sediment traps are plotted in Fig. 3. Traps from the upper growth zone ranged from  $3.36 \times 10^3$  cells  $\text{mm}^{-2}$  on day 4 to  $4.50 \times 10^4$  on day 20 ( $\bar{x} = 2.36 \times 10^4$ ), whereas lower traps ranged from  $1.85 \times$

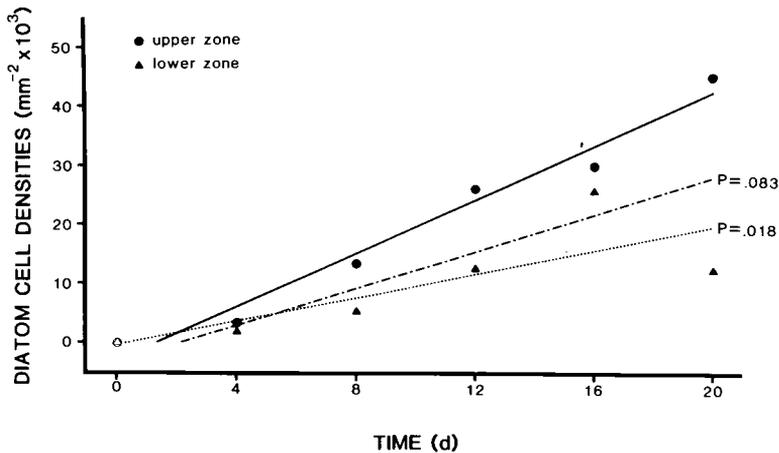


Fig. 2.3. Cumulative sediment trap diatom cell densities ( $\text{mm}^{-2} \times 10^3$ ), 22 June-12 July, 1984, from upper ( $\bullet$ ) and lower ( $\blacktriangle$ ; --- excluding 20d value; - - - including 20d value) growth zones. P-values indicate the comparison of slopes between the two zones.

TABLE 2.6

Percent planktonic diatoms in 4d instantaneous and cumulative sediment traps in the upper (U) and lower (L) growth zones.

Date	4d Traps		Cumulative Traps	
	U	L	U	L
6/26	65.2	59.4	65.2	59.4
6/30	34.4	46.2	71.8	57.0
7/4	56.2	49.2	60.0	54.8
7/8	35.6	-	56.8	60.0
7/12	63.2	60.4	66.8	56.4
$\bar{x}$	50.9	53.8	64.1	57.5
S			29.4	10.8

$10^3$  cells  $\text{mm}^{-2}$  on day 4 to  $2.56 \times 10^4$  on day 16 ( $\bar{x} = 1.15 \times 10^4$ ). A comparison of the slopes of regression lines of densities from each zone demonstrated that sediment trap accumulation rates (impingement rates) in the upper growth zone were greater than in the lower zone ( $p = 0.018$ , see Fig. 3 legend).

A significantly greater percentage of planktonic diatoms was found in upper (64%) versus lower (58%) growth zone traps (Table 6), based on cumulative impingement samples (t-test;  $p < 0.05$ ,  $n=10$ ). No statistically significant difference was evident based on 4d traps however.

### 2.3.3 Storm effects

Storm-induced wave action and below surface turbulence resulted in significant losses of epilithic diatom cells. Reductions in unscraped rock densities were particularly dramatic, resulting in a 47% decline after the first storm and a 10% decline following a series of lesser storms beginning on day 16 (Fig. 4). Although unscraped rock samples were semi-quantitative, the standard deviation about the mean of three replicates was less than those from ringed samples collected on the same dates (cf. Fig. 2). Comparison of the overall mean of unscraped rock densities before storms ( $1.45 \times 10^5$  diatom cells  $\text{mm}^{-2}$ ,  $n=9$ ) versus after storms ( $1.05 \times 10^5$  diatom cells  $\text{mm}^{-2}$ ,  $n=6$ ) indicated a significant difference between the two (t-test;  $p < 0.05$ ). Due to the confounding effects of colonization and microsuccession on ringed and unringed rock surfaces, beginning with near zero densities, before versus after storm mean comparisons were not performed.

The percentages of planktonic diatoms found on unscraped rock, unringed rock, and in 4d sediment traps are listed in Table 7. Planktonic diatom densities (particularly *Fragilaria vaucheriae*) were significantly higher on rock surfaces prior to storms, particularly those supporting "ambient" community densities.

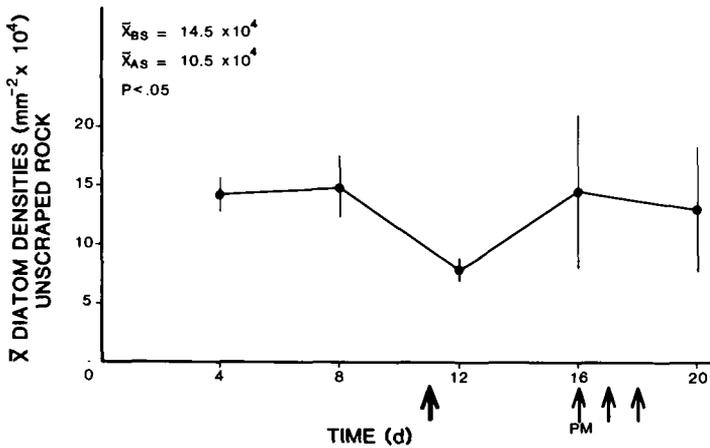


Fig. 2.4. Unscraped rock mean diatom densities ( $\text{mm}^{-2} \times 10^4$ ), demonstrating the effects of storm-induced turbulence (arrows indicate storm events, with larger arrow prior to 12d sample indicating a major storm; 16d samples collected at 1500hr, prior to evening storm designated by PM). Upper left: mean before and after storm values; \* $P < 0.05$ ;  $n = 3$ ;  $\pm 1$  SD.

Before the first storm, 78% of the diatoms from unscraped rock samples were planktonic as compared to 48% after the storm. Similarly, unringed rock communities were 64% planktonic before and 33% after the first storm.

In contrast, 4d sediment trap plankton percentages were numerically lower before than after storms in the upper growth zone. Although the difference was not statistically significant at the 0.05 level, this was likely due to a low number of samples ( $n=5$ ). Prior to the first storm, 34% of the 4d trap material

TABLE 2.7

Mean percent planktonic diatoms in unscraped rock, unringed rock, and 4d sediment trap samples before and after storms<sup>1</sup>.

Collection	Before Storms	After Storms	Comparison <sup>2</sup>
Unscraped Rock <sup>3</sup>	64	42	$p < 0.01^*$
Unringed Rock <sup>3</sup>	49	40	$p < 0.05^*$
Sediment Trap(4d)	45	60	$p > 0.05$

<sup>1</sup>Before storm dates: 6/26, 6/30, 7/8; After: 7/4, 7/12

<sup>2</sup>t-test

\*Indicates significant difference

<sup>3</sup>Upper growth zone

was comprised of planktonic diatoms, whereas 56% were planktonic after the first storm.

The percentage of nonliving diatoms on rock surfaces tended to increase during calm periods prior to storms. The mean percentage on unringed rock substrates was 28% before versus 21% after storm disturbances; the overall difference was significant at the 0.05 level. Comparable percentages of 29% before and 25% after storms were found on unscrapped rock surfaces, however the means were not statistically significant at the aforementioned level ( $0.10 > p > 0.05$ ).

## 2.4 DISCUSSION

### 2.4.1 Recolonization

Referring back to the simple model in Figure 1, it is clear that impingement of cells from the water column was more important in the recolonization of denuded rock surfaces than was direct encroachment from adjacent populations. If encroachment had contributed significantly to recolonization, then (1) unringed substrate cell densities should have exceeded ringed substrate densities, since the latter treatment precluded direct encroachment, and/or (2) community composition should have differed significantly between the two treatments. The results do not support either contention. Data in Fig. 2 demonstrate that there was no quantitative difference between unringed and ringed substrate samples throughout the study period. Moreover, little or no qualitative difference was found between the two treatments. Taxa that were unique to either sample type were rare in occurrence and exhibited no recognizable growth habit pattern. Furthermore, an overall comparison of general growth habits revealed no significance difference between ringed and unringed samples (Table 3).

Impingement of cells from the water column appeared to contribute significantly to the recolonization of denuded rock areas. Diatom accumulation rates were high in sediment traps when compared to rock surfaces being recolonized, particularly when values from the upper growth zone traps were used in the comparison (Table 4). This was exemplified by the fact that the 4d sediment trap density was actually greater than the 4d unringed substrate density over the same time increment. That is, recolonization of denuded rock surfaces could be accounted for on the basis of daily impingement rates alone. In addition, floristic differences between surfaces undergoing recolonization and sediment trap samples were not striking. Fewer than 20% of the 67 diatom taxa identified from ringed and unringed samples did not occur in sediment trap samples. Again, those taxa were typically rare in abundance and encountered as single valves in only one count. Considering the variability among replicate samples with respect to the diatom taxa found, the 20% value would seem of even lesser

importance.

Not surprisingly, unequivocal differences were found between impingement rates in traps from the upper (epilithic) zone versus the lower (pelagic) zone. One would presumably find rate differences based on the influence of the "local" flora in each zone, however the precise nature of the dissimilarity is not intuitive. Two basic differences were observed. First, the rate of impingement was greater in the upper versus the lower zone (Fig. 3). In contrast, Reynolds (1976) found relatively large numbers of cells in traps suspended in deeper waters. The present findings could not be attributed to a disproportionate number of resuspended, nonliving diatom frustules being redeposited in one zone or the other, since the percentage of nonliving cells remained rather constant among all samples (ca. 25%; Table 5).

Second, the percentages of planktonic diatoms were greater in upper versus lower growth zone cumulative samples (Table 6). (Although not all sediment trap collections were analyzed for nonliving diatoms, no consistent difference between the two zones was evident on that basis). Interestingly, the dominant planktonic diatom involved was Fragilaria vaucheriae, a taxon which has also been found in the periphyton in colonial rosettes attached to the substrate (Hoagland et al., 1982). The variability in its growth habit has in part led to its uncertain taxonomic status (Petersen, 1938).

Although such differences between zones in a lake or reservoir have not been reported, the exchange of individuals between the plankton and periphyton has been described. Brown and Austin (1973) found a decline in the planktonic diatom Fragilaria crotonensis with a coincident rise in its abundance in the periphyton, suggesting a settling. Similarly, Moss (1981) reported that, "...particularly in the cases of Diatoma elongatum and Synedra sp., it appears that species which are numerically predominant in the plankton at certain times of the year are also numerically abundant or predominant at the same or other times in the periphyton." Kairesalo (1976) also described an inverse relationship between the littoral phytoplankton and the epilithon in oligotrophic Lake Pääjärvi. The disappearance of loosely attached species, their resuspension in the water column and subsequent resettling onto colonized surfaces was proposed by Hudon and Bourget (1983), in a model based on observations from plastic panels placed in an estuary. Apart from these studies, little else has been reported concerning the potential source of colonizers on littoral substrates, despite the voluminous studies on periphyton community composition and the classical papers on the source of the spring plankton pulse (Lund, 1954; 1955).

A pertinent question to pose in light of these results is do such denuded areas on rocks represent an ecologically realistic situation? In addition to studies that have noted the occurrence of peeling or sloughing of the periphyton in other habitats (King and Ball, 1966; Castenholz, 1961), particularly as a

result of wave action (Young, 1945; Kairesalo, 1976; Hoagland, 1983), this substantial loss of the attached biofilm has also been reported for McConaughy reservoir (Roemer et al., 1984). Observations using SCUBA indicated that sloughing occurs in a patchy manner under conditions of low turbulence. This kind of biomass removal has been discussed for marine habitats as well (e.g., Yodzis, 1978; Sousa, 1979). By brushing relatively small areas clear of periphyton biomass, the methods employed in this study have presumably removed portions of the community in a similar, patchy manner. The size, distribution, and temporal frequency of natural patches have not been examined in freshwater attached communities.

The use of intact, natural substrates also supports the ecological realism of the present study methods. The substrates were clearly located in an ecologically relevant position and were identical in composition to surrounding surfaces, both conditions of concern in studies of this nature (Wetzel, 1965; 1983). Moreover, the introduction of "gaps" in the attached community may be more pertinent in marine and freshwater studies than the use of clean artificial substrates for investigating colonization and succession phenomena. Artificial surfaces, particularly when suspended from buoys or other openwater structures, likely function as ecological islands (Henebry and Cairns, 1980; Osman, 1982; see however Stewart et al., 1985), whereas denuded areas on existing substrates may be, for example, more analogous to tree gaps (e.g., Denslow, 1980) or badger disturbances (Platt, 1975). Secondary successions are likely a more common occurrence in the periphyton than primary successions, given the area of substrate surface available for attachment throughout the growing season. At present, our lack of understanding of the scales involved which separate colonizers from potential sites, both temporally and spatially, precludes any conclusions concerning the suitability of a particular experimental design in the field. The results presented here argue for the similarity between the "gap" and "island" approach, since impingement contributed far more to recolonization than encroachment, however final determination of the extent to which these findings apply to other aquatic systems awaits further research.

#### 2.4.2 Storm effects

Wind-induced turbulence had a dramatic effect on the structure and dynamics of the unscraped epilithic community (Fig. 4). Direct underwater observations confirmed that turbulence resulted in a visibly reduced biofilm thickness on all rock surfaces down to ca. 3.5m, coincident with an increase in water turbidity due to suspended cells and detritus. It is interesting to note that the younger communities (4-12d) from ringed and unringed substrates were apparently unaffected by turbulence, whereas the relatively older communities (16-20d) were significantly impacted (Fig. 2). These results are consistent with previous

observations made on communities of a similar composition from a eutrophic reservoir (Hoagland, 1983). Presumably when diatom cell densities and the vertical stature of the community are relatively great, the biofilm is physically more susceptible to dislodging depending upon the degree of turbulence. The importance of disturbance in the marine rocky intertidal zone is well established (Lewis, 1977; Sousa, 1984; Dethier, 1984), but has not been adequately addressed in fresh waters.

Of equal importance perhaps is the differential effect that storm activity had on planktonic versus periphytic diatoms. The proportion of planktonic diatoms on unscraped and unringed surfaces was significantly greater before storms than after and vice versa for sediment trap samples to a lesser degree (Table 7). This strongly suggests that the planktonic members of the periphyton, or the tychoplankton (Round, 1981), were more greatly affected by turbulence during storm events than the true periphytic forms which produce permanent attachment structures (stalks, pads, etc.). That is, the free-floating members of the attached community were dislodged from the substrate and subsequently deposited in the 4d sediment traps during each storm event, to a greater extent than sessile forms. This reduction was preferential and therefore not random among species in the community as indicated by Peterson (1977) in his model to examine the relationship between perturbations and diversity, or equal as suggested by Robinson and Sandgren (1983) in their experimental manipulations of plankton microcosms.

These results are consistent with those of Kuhn et al. (1981) who hypothesized that planktonic populations in the periphyton are maintained primarily by invasion pressure. Similarly, Jones (1978) found that the ability of planktonic forms to establish on polyurethane foam "islands" determined the pattern of early colonization. In addition, this type of large scale upwelling and subsequent settling of pseudoplanktonic and pseudoperiphytic diatoms following turbulence events may in part explain the increases in sediment trap densities seen by Reynolds (1976) during calm periods, rather than turbulence-related differences in trapping efficiencies.

Although diatom colonization is probably the most poorly understood process of the fouling sequence in marine systems (see Callow and Evans, 1981), it is even less known in fresh waters. Aside from the process of recolonization of substrates during the growing season, the actual source of the initial spring diatom bloom common in many bodies of fresh water remains basically unknown. As Yodzis (1978) pointed out, "...dispersal is a dynamic element of competition for space," a notion that certainly warrants further research in sessile systems.

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