

Zooplankton Grazing Activity and Assimilation in the Presence of Mount St. Helens Ash

Abstract

Experiments were conducted to determine the effects of the particulate fraction of Mt. St. Helens ash on ingestion rate, filtration rate, and assimilation efficiency of *Diatomus ashlandi* Marsh and *Daphnia pulex* Leydig. When fed *Cryptomonas* together with ash, grazing activity by both zooplankters, was not affected. When fed *Cyclotella* with small amounts of ash, *Daphnia* ingested more algae whereas *Diatomus* did not. Ash interfered with the assimilation of carbon-14 by *Daphnia* ingesting *Cyclotella*.

Introduction

The volcanic eruption of Mt. St. Helens on 18 May 1980 produced tons of ash and debris to be carried eastward by prevailing winds. More than 30 lakes in the immediate vicinity of the eruption sustained altered physical, chemical, and biological characteristics because of ash deposition (Dion and Embrey 1980). The ash was deposited in various amounts over Washington, Idaho, Oregon, and Montana (Sarna-Wojcicki *et al.* 1980), suggesting that surface waters of the Pacific Northwest will contain suspended ash particles for many years to come. Seasonal runoff and sediment mixing are primary factors determining the amount of ash that will be present in the water column, and particles less than 20 μm in diameter are likely to remain suspended for long periods.

Frutcher *et al.* (1980) have characterized both the particulate and soluble fractions of the ash, whereas Pereira *et al.* (1982) focused on organic contaminants. Of course, filter-feeding zooplankton may be directly affected by the particulates because of the nature of their feeding mechanism. Furthermore, increases in the ash-phytoplankton ratio may alter the ingestion rate through selectivity, as well as the assimilation efficiency by changing physical and chemical properties of gut contents. Many investigators have studied zooplankton preference for both large cells (Burns 1968, 1969a; Hargis 1977; Arnold 1971) and small cells (Hadas 1982, Burns 1969b, Vanderploeg 1981) in order to clarify the complex pattern of particle size selection, a pattern that could be altered in the presence of ash particles. Although dissolved components are many,

virtually all of the ash is insoluble in water. In this study we examined the particulate fraction of Mount St. Helens ash for its effects on filtration rate, ingestion rate, and assimilation efficiency of two filter-feeding zooplankters, *Diatomus ashlandi* Marsh and *Daphnia pulex* Leydig, using *Cyclotella meneghiniana* Kütz, a 500 μm^3 centric diatom, and *Cryptomonas ovata* Ehr., a 1000 μm^3 ovoid flagellate as food sources.

Methods

Mount St. Helens ash, collected 18 May 1980 at Pullman, Washington, was used in experiments after 10 g l⁻¹ was allowed to settle undisturbed in deionized distilled water at 20°C for 72 h. The ash suspension was then removed from settled material by siphoning and filtered through a 0.2 μm - 24 mm membrane. The ash/filter cake was washed copiously with distilled water and concentrated by backflushing the ash with synthetic medium (Rees 1979). A mean concentration was determined by vacuum drying five 1-ml samples at 65°C for three h then weighing. The concentrated suspension (~1.9 mg ml⁻¹) was stored at 5°C in the dark for approximately one week before using.

Cyclotella meneghiniana Kütz (clone CyOH2 obtained from S.S. Kilham) and *Cryptomonas ovata* Ehr. (Texas Culture Collection UTEX #358) were maintained in Rees's medium at 20°C with a photoperiod of 15L:9D under 0.35 ly h⁻¹ of cool white fluorescent light. Algal cell cultures were acclimatized to the appropriate light temperature conditions for 24 h prior to experiments.

Daphnia pulex Leydig and *Diaptomas ashlandi* Marsh were collected from Rock Lake, Washington, and maintained in Rees's medium at 14°C with a light flux of 0.70 ly h⁻¹. All experiments concerning the ash-zooplankton interaction were carried out under 0.70 ly h⁻¹ at 8°, 14°, and 20° C unless noted otherwise. Experimental animals were acclimatized to their respective test temperatures for 14 days to allow stabilization of metabolic activity (Hargis 1977). *Cyclotella* was supplied weekly as a primary food source, but bacteria and other algal contaminants likely were also present. Male and female (gravid or non-gravid) animals were selected at random for all experiments.

Algal cells were labeled radioactively by adding 50 ml of 1 µCi ml⁻¹ ¹⁴C-NaHCO₃ to 100 ml of culture. The cultures were placed under continuous 1.40 ly h⁻¹ illumination for 48 h at 20°C, then harvested by centrifugation, washed three times, and resuspended in Rees's medium. The cells were incubated overnight at the test temperatures prior to experiments. Triplicate 20-ml samples were filtered, digested, and counted to determine mean specific activity.

For *Diaptomus* or *Daphnia*, the effects of particulate ash on ingestion rate, filtration rate, and assimilation rate were tested using four concentrations of ash (0, 10, 50, and 250 mg l⁻¹) mixed with labeled unialgal suspensions of *Cryptomonas* or *Cyclotella*. The four grazing experiments (2 zooplankton species x 2 phytoplankton species) were replicated six times. The procedure involved placement of 20 diaptomids or 10 daphnids in 125-ml Erlenmeyer flasks containing 25 ml Rees's medium for 15 h prior to experiments. No food was provided during this period. Then 20 ml of the labeled algal suspension were added while simultaneously adding concentrated ash. Rees's medium also was added to bring the final volume to 60 ml. Each replicate consisted of 12 flasks (4 ash concentrations x 3 temperatures).

The feeding times in labeled-cell suspensions were critical. Test periods should be shorter than the time to first egestion of labeled cells (Richman 1966, Schindler 1968, and Kibby 1971). Hargis (1977) provided a time-course study for *Diaptomus ashlandi* showing 30 min to first egestion. In our experiments, the animals were allowed to feed for 10 min as suggested by Krylov (1981). One half of the number of animals present in each flask was then removed by pipette and filtered onto GF/C glass fiber filters. Each

filter was placed in a scintillation vial to which 1 ml of tissue solublizer was immediately added. After 24 h digestion, the samples were counted to estimate ingestion. The remaining animals were placed into unlabeled cell suspensions of the same concentration. After feeding for 5 h, they were removed by filtering with Nitex mesh, digested, and counted. The assimilation efficiency was estimated by calculating the ratio of animal radioactivity after 5 h of gut clearance to the total radioactivity ingested in 10 min. Filtration rates were estimated by the equation:

$$FR = \frac{\text{dpm mg}^{-1}}{\text{dpm ml}^{-1}} \times \frac{60 \text{ min h}^{-1}}{T \text{ min}}$$

where FR is filtration rate (ml mg⁻¹ h⁻¹) and T is duration of the labeled feeding period. The ingestion rate (cells mg⁻¹ h⁻¹) is the product of food density (cells ml⁻¹) and FR. Food density (cells ml⁻¹) determined by averaging 10 haemocytometer counts) was kept between 25,000-500,000 which is reported to produce a constant ingestion rate (Richman 1966). Live and dead animal controls for self-absorption of radioactivity were considered to be insignificant as reported in similar feeding experiments (Richman 1966).

Results and Discussion

Ash Characterization

The composition of ash used in experiments and characterized by x-ray fractionization (Geology Department, Washington State University) was SiO₂-67.0, Al₂O₃-17.1, TiO₂-0.6, Fe₂O₃-1.9, FeO-2.1, MnO-0.1, CaO 4.3, MgO-1.6, K₂O-1.6, Na₂O-3.6, P₂O₅-0.2 percent. Settling reduced the suspended particulate fraction to approximately 30 mg l⁻¹, 96 percent of the particles with volumes less than 9µm. Microscopic examination of water samples from nearby lakes revealed the presence of many particles larger than those left in laboratory suspensions, suggesting that re-suspension caused by wind and currents is common.

Grazing by Zooplankton

Table 1 presents mean filtration, ingestion, and assimilation rates over all treatments (ash level, temperature) for each replicate by experiment. Although chemical and physical conditions were virtually constant among replicates, variability within experiments still was very high. Clearly,

TABLE 1. Mean filtration (ml mg⁻¹ h⁻¹), ingestion (10⁵ cells mg⁻¹ h⁻¹), and assimilation percentage for each replicate.

Experiment	Replicate					
	1	2	3	4	5	6
<i>Diaptomus-Cryptomonas</i>						
Filtration	17.6	18.1	6.2	5.7	5.2	2.9
Ingestion	5.4	5.6	2.4	2.2	2.0	1.1
Efficiency	20.1	28.8	27.4	36.2	30.4	53.0
<i>Daphnia-Cryptomonas</i>						
Filtration	13.1	12.3	1.0	.7	13.3	14.9
Ingestion	9.8	8.9	.3	.2	6.8	7.6
Efficiency	63.0	78.4	61.9	79.3	31.4	31.9
<i>Diaptomus-Cyclotella</i>						
Filtration	10.5	9.0	33.7	60.6	4.3	4.6
Ingestion	4.6	3.9	1520.0	2740.0	61.8	66.0
Efficiency	51.0	55.5	29.1	26.2	44.3	30.7
<i>Daphnia-Cyclotella</i>						
Filtration	.2	.3	10.6	11.4	6.4	5.6
Ingestion	.6	.8	41.4	44.5	64.8	56.6
Efficiency	38.4	30.2	24.5	28.3	20.5	27.6

condition of the algal food, as well as animal age and size, may affect grazing activity. For example, daphnids feeding on cryptomonads in replicates 3 and 4 were much smaller than those utilized in other replicates (Table 2), and there are substantial differences in filtration and ingestion rates. These results are contrary to those

TABLE 2. Mean animal dry weight (μg) by feeding experiment for each replicate.

Experiment	Replicate		
	1,2	3,4	5,6
<i>Diaptomus-Cryptomonas</i>	14.0	3.1	6.1
<i>Daphnia-Cryptomonas</i>	1950.0	10.9	94.0
<i>Diaptomus-Cyclotella</i>	14.0	3.1	5.2
<i>Daphnia-Cyclotella</i>	17.5	24.1	5.0

of Burns (1968, 1969b). Also, the small copepods used to test for effects of particulate ash when fed *Cyclotella* were considerably more active than the larger animals used in replicates 1 and 2 (Table 1).

Replicate variability was removed by making all observations for a given replicate relative to the mean for that replicate. The subsequent analyses of variance are summarized in Table 3. Although there were six replicates for each ex-

TABLE 3. Analysis of variance (F-values) for feeding experiments: #1 *Diaptomus-Cryptomonas* (See Table 4), #2 *Daphnia-Cryptomonas*, #3 *Diaptomus-Cyclotella* (see Table 5), #4 *Daphnia-Cyclotella* (see Table 6). Error term has 56 degrees of freedom.

Effect	d.f.	Experiment #			
		1	2	3	4
<i>Filtration or Ingestion</i>					
Ash (A)	3	2.62	.41	1.34	3.49*
Temperature (T)	2	.74	.73	2.94	4.28*
A x T	6	.79	.64	1.03	1.24
<i>Assimilation</i>					
Ash (A)	3	.32	1.19	.93	3.46*
Temperature (T)	2	1.69	.51	3.18*	.70
A x T	6	.76	.69	1.83	.73

* P < .05

periment, only one light flux (0.70 ly h⁻¹) was used at each of the three experimental temperatures. Consequently, 56 degrees of freedom were available for the error term in analysis of variance (ANOVA) tests of significance.

Diaptomus-Cryptomonas (Experiment #1)

Since food concentration was the same for all treatments within each replicate, ingestion rate is always a constant times filtration rate and ANOVA results are the same for both. No consistent effect of particulate ash was detected for filtration/ingestion nor was a significant effect found for assimilation (Table 3). There is the suggestion of a temperature effect on filtration/ingestion (Table 4), perhaps highest at 14°C (P ~ .06).

TABLE 4. Relative filtration, ingestion, and assimilation of *Cryptomonas* by *Diaptomus* in the presence of particulate ash (means for six replicates).

	Temperature (°C)	Particulate Level (mg l ⁻¹)			
		0	10	50	250
<i>Filtration or Ingestion</i>					
	8	1.02	.58	1.15	.78
	14	1.19	1.33	1.22	.98
	20	1.00	.89	.91	.90
Mean		1.07	.93	1.09	.90
<i>Assimilation</i>					
	8	1.47	1.50	.91	.90
	14	1.11	.77	.93	1.09
	20	.70	.88	.81	.93
Mean		1.09	1.05	.88	.97

Daphnia-Cryptomonas (Experiment #2)

No evidence for an effect of ash on cryptomonad grazing by *Daphnia* was found and none is supported by ANOVA (Table 3). Apparently the presence of ash did not influence the feeding behavior of *Daphnia*.

Diaptomus-Cyclotella (Experiment #3)

Temperature apparently affected assimilation rate, with highest values at 14°C (Tables 3 and 5). There was also the suggestion of a temperature effect on filtration/ingestion, but as with experiment 2, ash particles did not alter grazing activity.

TABLE 5. Relative filtration, ingestion, and assimilation of *Cyclotella* by *Diaptomus* in the presence of particulate ash (means for six replicates).

	Temperature (°C)	Particulate Level (mg l ⁻¹)			
		0	10	50	250
Filtration or Ingestion	8	1.38	1.22	1.62	.63
	14	.74	.69	.88	.76
	20	.76	.95	1.24	1.14
Mean		.96	.96	1.25	.84
Assimilation	8	.77	.87	1.10	1.13
	14	1.89	1.12	1.01	1.89
	20	.92	.95	.61	.74
Mean		1.19	.98	.91	.92

Daphnia-Cyclotella (Experiment #4)

Filtration/ingestion was affected by both temperature and by ash (Tables 3 and 6). The highest rates occurred at 20° C and at intermediate ash concentration. Assimilation, on the other hand, was only affected by the presence of ash. Here the ash particles apparently interfered with assimilation in that the rate at the highest ash level was reduced to approximately half of that measured when no ash was present (Table 6).

Two additional experiments, in triplicate, were run at 14°C using *Daphnia* in an effort to support these results; one experiment involved *Cryptomonas* and the other experiment involved *Cyclotella*. Ash levels used were as before. This time, at one temperature, assimilation of both

Cryptomonas and *Cyclotella* was adversely affected by the ash (Table 7).

TABLE 6. Relative filtration, ingestion, and assimilation of *Cyclotella* by *Daphnia* in the presence of particulate ash (means for six replicates).

	Temperature (°C)	Particulate Level (mg l ⁻¹)			
		0	10	50	250
Filtration or Ingestion	8	.88	1.15	.97	.69
	14	.64	.90	.97	.93
	20	.93	1.28	1.72	.93
Mean		.82	1.11	1.22	.85
Assimilation	8	1.32	1.31	1.23	.61
	14	1.44	.93	.65	.77
	20	1.26	.90	.78	.82
Mean		1.34	1.05	.88	.73

TABLE 7. Relative filtration, ingestion, and assimilation by *Daphnia* at 14°C.

		Particulate Level (mg l ⁻¹)			
		0	10	50	250
<i>Cryptomonas</i>					
Filtration of	Ingestion	.71	1.06	1.00	1.23
Assimilation		1.29	1.08	1.04	.59
<i>Cyclotella</i>					
Filtration or	Ingestion	1.04	1.11	1.05	.81
Assimilation		1.18	1.00	.80	.94

There is a wealth of literature dealing with filtration and associated assimilation by microcrustaceans feeding on phytoplankton in the absence of inert particles (Wetzel 1983). In general, our values fall within the range of reported results, although some extremely high rates of filtration were observed for *Daphnia* feeding on *Cyclotella* (Table 1). Closer to our objectives, Edmondson (1984) reviewed broadly the many possible effects of volcanic ash in lakes, hence a lengthy discussion here would be redundant. He does point out, however, that some species of *Daphnia* are able to live for long periods in ponds made turbid by silt and clay. Furthermore, crustaceans and rotifers in Soap Lake and Lake Lenore, Washington, carried on with their normal seasonal changes following heavy ash fall (Edmondson and Litt 1984). It is not surprising, therefore, that grazing in our

study by *Diaptomus* and *Daphnia* on *Cryptomonas* was not altered significantly by the presence of particulate ash, a conclusion that applies equally to *Diaptomus* feeding on *Cyclotella*.

Mechanisms responsible for these limited effects have not been identified, although ash particles ingested with phytoplankton probably would reduce assimilation by limiting the amount of digestible algal material in contact with the gut wall. Further speculation suggests that intermediate ash concentrations might increase filtration in response to metabolic demand,

whereas very large concentrations might cause *Daphnia* to avoid these foreign particles, thereby overriding demand.

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Literature Cited

- Arnold, D. E. 1971. Ingestion, assimilation, survival and reproduction by *Daphnia pulex* fed seven species of blue-green algae. *Limnol. Oceanogr.* 16:906-920.
- Burns, C. W. 1968. The relationship between body size of filter-feeding Cladocerans and the maximum size of particle ingested. *Limnol. Oceanogr.* 13:675-678.
- _____. 1969a. Particle size and sedimentation in the feeding behavior of two species of *Daphnia*. *Limnol. Oceanogr.* 14:392-402.
- _____. 1969b. Relation between filtering rate, temperature, and body size in four species of *Daphnia*. *Limnol. Oceanogr.* 14:693-700.
- Dion, N. P., and S. S. Embrey. 1980. Effects of Mount St. Helens eruption on selected lakes in Washington. U.S. Geol. Surv. Circ. 850-C.
- Edmondson, W. T. 1984. Volcanic ash in lakes. *Northw. Env. J.* 1:139-150.
- _____, and A. H. Litt. 1984. Mt. St. Helens ashfall in the lower Grand Coulee, Washington State. *Verh. Internat. Verein. Limnol.* 22:510-512.
- Frutcher, J. S., D. E. Robertson, J. C. Evans, K. B. Olsen, E. A. Lepel, J. C. Laul, K. H. Abel, R. W. Sanders, P. O. Jackson, N. S. Wogman, R. W. Perkins, H. H. Van Tuyl, R. H. Beauchamp, J. W. Shade, J. L. Daniel, R. L. Erikson, G. A. Schmel, R. N. Lee, A. V. Robinson, O. R. Moss, J. K. Briant, and W. C. Cannon. 1980. Mount St. Helens ash from the May 18, 1980 eruption: chemical, physical, mineralogical, and biological properties. *Science* 209:1116-1125.
- Hadas, O., B. Z. Cavari, Y. Kott, and U. Bachrach. 1982. Preferential feeding behavior of *Daphnia magna*. *Hydrobiologia* 89:49-52.
- Hargis, J. R. 1977. Trophic processes involved in aquatic secondary productivity. Washington State University. Dissertation.
- Kibby, H. V. 1971. Energetics and population dynamics of *Diaptomus gracilis*. *Ecol. Monogr.* 41:311-327.
- Krylov, P. I. 1981. Radioisotopic methods for study of the nutrition of zooplankton and its transformation of food energy. *Hydrobiol. J.* 16:52-68.
- Pereira, W. E., C. E. Rostad, H. E. Taylor, and J. M. Klein. 1982. Characterization of organic contaminants in environmental samples associated with Mt. St. Helens 1980 volcanic eruption. *Env. Sci. Technol.* 16:387-396.
- Rees, J. T. 1979. Community development in freshwater microcosms. *Hydrobiologia.* 63:113-128.
- Richman, S. 1966. The effect of phytoplankton concentration on the feeding rate of *Diaptomus oregonensis*. *Verh. Internat. Verein. Limnol.* 16:392-398.
- Sarna-Wojcicki, A. M., S. Shipley, R. B. Waitt, D. Dzurisin, W. H. Hays, J. O. Davis, S. H. Wood, and Thomas Bateridge. 1980. Areal distribution, thickness, and volume of downwind ash from the May 18, 1980, eruption of Mount St. Helens: U.S. Geol. Surv. Open-File Rep. 80-1078.
- Schindler, D. W. 1968. Feeding, assimilation, and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. *J. Anim. Ecol.* 37:369-385.
- Vanderploeg, H. A. 1981. Seasonal particle size selection by *Diaptomus sicilis* in offshore Lake Michigan. *Can. J. Fish. Aquat. Sci.* 38:504-517.
- Wetzel, R. G. 1983. *Limnology*. W. B. Saunders, Philadelphia.

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