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The diatoms ingested by freshwater snails: temporal, spatial, and interspecific variation

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Abstract

Seventeen species of diatoms, representing a broad range of sizes, shapes, and growth habits, were collected from rocks in rapidly-flowing sections of the Mitchell River, North Carolina. The diatoms ingested by adult *Goniobasis proxima*, juvenile *Leptoxis carinata*, and adult *Physa* sp. co-occurring in this habitat were indistinguishable from one another, in spite of great differences in radular morphology. All snails sampled the diatom flora almost randomly, with only one or two of the larger diatom species under-represented in the gut contents. Some snails also seemed to selectively ingest the smaller individuals of the larger diatom taxa, and larger individuals of the smaller diatom taxa. The diatoms identifiable in juvenile *Goniobasis* guts were somewhat more distinctive, although this seemed to be due at least partly to more mechanical breakage. The diatom flora of quiet, muddy pools was much different from that of shallow, rocky areas, but once again, *Goniobasis* seemed to sample the available flora randomly. Seasonal variation was also apparent in the diatom diet of *Goniobasis*. We suggest that in some cases, it may be reasonable to use snails to sample the diatom assemblage present in a particular habitat, if more direct methods are impractical.

Introduction

There is evidence that grazing by freshwater snails strongly influences periphyton communities, perhaps most directly by reducing biomass (Doremus & Harman, 1977; Kesler, 1981; Jacoby, 1985; Hawkins & Furnish, 1987). Freshwater snail grazing may stimulate primary production (Lamberti *et al.*, 1987), although most workers have reported a reduction (Hunter, 1980; Cuker, 1983; Mulholland *et al.*, 1983) or no change in production (Kehde & Wilhm, 1972; Sumner & McIntire, 1982). Gregory (1983) reported evidence that the loss of biomass to freshwater snail grazing may be compensated for by increased primary productivity in the algae left behind. Thus the net effect of grazing may be a function of snail density. Gross changes in community structure (e.g., dominance shifts between greens, blue-greens, single cells or filaments) have often been ascribed to grazing by freshwater snails (Kesler, 1981; Cuker, 1983; Gregory, 1983; Eichenberger *et al.*, 1984; Cattaneo & Kalff, 1986; Lamberti *et al.*, 1987; Lowe & Hunter, 1988; Power *et al.*, 1988). Further underscoring their importance, experimental reduction of freshwater snail density

in natural settings has resulted in increased abundance of other invertebrate grazers (Cattaneo & Kalff, 1986; Hawkins & Furnish, 1987).

Cummins & Klug (1979) suggested that diatoms are the critical nutritional components of the periphyton. Thus it is not surprising that snails seem to influence the structure of attached diatom communities. In particular, several authors have observed an increase in the relative abundance of *Cocconeis placentula* Ehr. under grazing pressure by snails (Patrick, 1970; Hunter, 1980; Kesler, 1981). Unlike most diatom taxa, *Cocconeis* cements itself flat on the surface of a hard substrate, and apparently avoids the scraping action of the snail's radula. Hunter (1980) reported that population densities of the smaller diatoms *Gomphonema* and *Navicula* were not as reduced by snail grazing as some larger species. Sumner & McIntire (1982) and Gregory (1983) also reported that the relative densities of smaller diatoms (especially *Achnanthes*) increased at the expense of larger taxa under heavy grazing pressure. To our knowledge, all the studies cited above have involved artificial substrates. But Thomas *et al.* (1985) compared ungrazed macrophyte leaves to strips grazed by the medically-important planorbid *Biomphalaria*. They reported phenomena similar to those outlined above: improved escape from grazing by the smaller *Achnanthes*, and the adpressed *Cocconeis* and *Amphora*.

Although it has been demonstrated that the impact of freshwater snails on a diatom community can be great, the nutritional importance of diatoms to snails is less clear. Detritus was by far the most common item in the guts of 20 species of freshwater snails collected from 24 habitats in England (Reavell, 1980). Algae of all sorts were present in the guts of over 80% of the species, but never accounted for more than 10% of the volume. The problems associated with the analysis of gut contents are well-known, however. For example, although detritus comprises the bulk of the gut contents of the pulmonate *Planorbis vortex* (L) in the wild, Lodge (1986) found evidence of selection against detritus and for diatoms. Calow (1973a; b) showed that the freshwater pulmonate limpet, *Ancylus fluviatilis* (Mull.), ignored detritus and fungal hyphae to selectively ingest periphytic algae, and that diatoms were preferred over green unicellular, green filamentous, or blue-green algae. There were preferences among diatom species in the laboratory, apparent most clearly in satiated snails. But Calow (1973a) did not observe an effect on diatom community structure in the field, probably because snails are not normally satiated. Calow & Fletcher (1972) estimated an assimilation efficiency of 88% for *A. fluviatilis* feeding on the diatom, *Navicula*. In contrast, it has been demonstrated that diatoms are not the preferred food of a number of freshwater snail species (Calow, 1970; 1974; Lodge, 1986). The actual importance of diatoms in the diets of freshwater snails is probably a complex function of snail, environment, and available foods.

The question addressed in this study is complementary to both these areas of research. We will not attempt to evaluate the importance of snails to the diatom flora, nor the importance of diatoms to snails. Rather, we examine differences in the diatoms ingested by snails of different age classes and species, and in different habitats and seasons, and compare these to diatom samples taken using more conventional techniques. In particular, Dillon (1984) used the similarity of diatoms ingested by the snail *Goniobasis proxima* (Say) as a measure of overall environmental similarity between 25 isolated streams in the southern Appalachians. Diatoms were found to be a large component of the material ingested by the snails in these habitats. The object of this investigation was to determine to what extent snails such as *G. proxima* sample the diatom flora randomly.

Methods

We selected the Mitchell River (a tributary of the Yadkin River, flowing south from the Blue Ridge) for this study, primarily because of the three species of freshwater snails co-occurring there. Various aspects of the general biology and life history of the prosobranch, *Goniobasis proxima*, have been described by Dillon (1984; 1988a;

1988b). The biology of a second prosobranch, *Leptoxis carinata* (Brug.), has been described by Aldridge (1982). These two members of the family Pleuroceridae are very similar in morphology and natural history, a principal difference being that *G. proxima* prefers smaller streams while *L. carinata* is most common on rocks in larger rivers. Their co-occurrence in the Mitchell River is unusual. Research done with other pleurocerid snails suggests that *Goniobasis* and *Leptoxis* are 'generalists', grazing on attached algae of all types, ingesting detritus and shredding dead leaves (Lang, 1968; Elwood & Nelson, 1972; Hawkins *et al.*, 1982; Mulholland *et al.*, 1983; 1985; Hawkins & Furnish, 1987). Elwood *et al.* (1981) have suggested, however, that *Goniobasis* may prefer diatoms, due to their lower C:N ratios. Dazo (1965) has reviewed the alimentary systems of pleurocerids. Particularly notable is a stomach sack containing a crystalline style, which grinds food against a gastric shield.

Also present in the Mitchell River is the pulmonate snail, *Physa*. (These snails belong to a group that has recently been split into the genus *Physella* (Te, 1980). This particular species may be *P. hendersoni* Clench.) Many aspects of the general biology of *Physa* (DeWitt, 1955; Clampitt, 1970; Dillon & Benfield, 1982) contrast strongly with *Goniobasis* and *Leptoxis*. Kesler *et al.* (1986) have described the alimentary system of *Physa*, characterizing it primarily as a detritivore but noting that diatoms may also be important in the diet. The stomach is not differentiated into style sack, crop, gizzard, or any other grinding organ.

We used the same sampling locality as Dillon (1984), approximately 25 km SE of Mt. Airy, Surry County, North Carolina. The Mitchell River is a fourth-order stream at this point (judging from USGS 7.5 minute topographic maps), and is broad, shallow, and rapidly flowing (approximately 10–15 m wide with approximately 2 m^3 sec^{-1} annual mean flow). The catchment upstream is almost entirely forested, with little agriculture and few inhabitants. The water is soft (about 5–10 mg l^{-1} Ca^{+2}, alkalinity 8–12 mg l^{-1}) and low in nutrients. At the four sampling dates of this study, temperatures were (mid-stream, mid-depth): summer 20.5 °C, fall 14.5 °C, winter 4.0 °C, spring 15.0 °C. A map locating the sample locality ('Mtch') is given in Dillon (1984), and additional seasonal physical and chemical data are available in Dillon (1982).

In April, 1981, we selected an apparently homogeneous single square foot (929 cm^2) of rocky bottom at midstream. Water flow was rapid and depth was approximately 5 cm. The site was not shaded. Snails were abundant, and very little material of any sort was visible on exposed rock surfaces. Grazing was probably intense. We collected 5 adult (shell length 1.5 to 2.0 cm) *Goniobasis proxima* and placed them immediately in a vial of 70% ethanol, which killed them tightly contracted in their shells. We also collected 10 juvenile *G. proxima* (one year olds, less than 1.0 cm), 10 juvenile *Leptoxis carinata* (one year olds), and 2 adult *Physa* (shell length over 1.0 cm), placing each type of snail in a separate vial. We also picked up several rocks from this square foot and scraped material from their surfaces into a vial with a scalpel.

A second site of one square foot was selected in a heavily shaded area near the bank of the stream. The water at this site was approximately 16 cm deep and calm, with an apparently homogeneous mud bottom. Here we collected 5 adult *Goniobasis* and sucked material from the surface of the mud with a Pasteur pipet. Snails were less common, but again, no macrophytes or macroscopic algae were apparent.

Samples of adult *Goniobasis* were also taken in July and October, 1980, and January, 1981. These were mixtures of 5 snails from riffles with rapidly-flowing water and 5 from calm, muddy pools.

In the laboratory, each snail was cleaned thoroughly with a brush and rinsed several times in distilled water. The shell of each individual was then cracked with pliers and the animal removed whole. The head-foot region, with operculum and any contaminating diatoms, was excised and retained for radula analysis. The remainder of the tissue, including stomach and intestine, was given a final distilled water rinse and combined with tissue from other snails from the sample.

Tissue (or substrate material) from each of the

ten samples was boiled in a solution of 10 ml concentrated nitric acid and 20 ml water. A period of about 30 minutes was sufficient to digest all tissue and clean the diatom frustules. Samples were rinsed, allowed to settle, aspirated 5–6 times to dilute residual acid, and preserved in 5% formalin. Slides were prepared by resuspending the frustules and evaporating them on cover slips, then mounting the cover slips with hyrax.

A total of 1500 diatom cells were identified initially from each of the ten samples, ignoring fragments of less than half a cell. Apical and transverse measurements were made on 30 randomly-selected whole cells of each diatom species identified, when available. After our initial analysis, a second set of counts was deemed necessary on the five samples from the riffle. In this second analysis, counts were made of both whole and partial diatom cells (less than half a frustule remaining) as they were randomly encountered, up to the point that 300 identifiable diatoms had been screened. Slides from all samples have been deposited at the Academy of Natural Sciences, Philadelphia.

The frequencies of individual diatom species in pairs of samples were compared using chi-square two-sample tests, corrected for continuity (Siegel, 1956: 107), or in the case of very low numbers, exact probability tests. Because a comparison between any two samples typically involved about 17–20 such tests (one test per diatom species), we used the sequential Bonferroni technique to evaluate significance (Holm, 1979; Rice, 1989). To reject the null hypothesis at 95% confidence, we required an initial value of chi-square significant at the $0.05/17 = 0.0003$ level (for example), subsequently adjusted. An identical procedure was used to compare riffle substrate and gut contents in the proportions of broken diatom frustules they contained, but with 4 generic categories, rather than the larger number of specific categories. Mean sizes of the 10 most common diatom species on the riffle substrate were compared to those in snail guts using t-tests, assuming unequal variances (Sokal & Rohlf, 1969: 376). Tests were two-tailed, and again, a level of 0.05 was set for rejection of the null hypothesis, initially requiring a nominal P value of $0.05/10 = 0.005$ by the Bonferroni criterion.

The buccal mass was dissected from the tissue saved from selected snails and immersed in commercial bleach to clean the radula. Measurements were taken of the length and width of the entire radular ribbon, as well as the sizes of individual teeth and distances between cusps, using an ocular micrometer.

Results

Example radulae from the snails collected in the Mitchell River are shown in Fig. 1. No significant

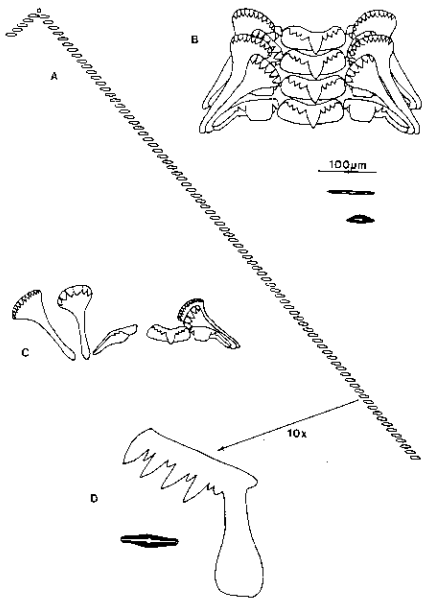

Fig. 1. Scale drawings of radulae and diatom frustules. (A) Schematic of a partial row from the radular ribbon of *Physa*. (B) Several rows from the radula of adult *Goniobasis*, in natural arrangement. Frustules of *Synedra ulna* (above) and *Cymbella tumida* (below) supplied for comparison. (C) One row from the radula of juvenile *Goniobasis* or *Leptoxis*. Several individual teeth are separated to show detail. (D) A single tooth from the radula of *Physa*, magnified 10×. The outline of an *Achnanthes minutissima* is below.

difference was noticed between the radulae of *G. proxima* and *L. carinata* and those of other pleurocerids previously described. *Goniobasis* and *Leptoxis* have 'taenioglossate' radulae – seven teeth (of four types) per row. Adult *Goniobasis* had about 80 rows of teeth (discounting those under formation) on a ribbon about 1.2–1.7 mm long and 300–400 micrometres wide. Juvenile *Goniobasis* and *Leptoxis* had about 60 rows of fully-formed teeth on ribbons about 0.8–1.1 mm long and 200–300 micrometres wide. The radular ribbon of *Physa*, by contrast, was wider than it was long. About 120–160 small, uniform teeth were found arranged in about 30 V-shaped rows on a ribbon 400–500 micrometres long but 1.5–2.0 mm wide. Although the *Physa* ribbon was an order of magnitude wider than that of *Goniobasis* or *Leptoxis*, the cusps on the teeth were an order of magnitude smaller.

A total of 21 diatom species were identified from April samples, considering all environments and collection methods (Table 1). The outlines of several example frustules are compared in scale to the radulae of the snails that graze upon them in Fig. 1. As may be seen in the figure, the radulae of *Goniobasis* and *Leptoxis* would seem scaled to ingest the rarer, larger diatoms (e.g., *Cymbella* and *Synedra*), whereas *Physa* seems equipped to ingest the smaller, more common diatoms (e.g., *Achnanthes*.)

In spite of the striking radular differences, there were no differences significant at the (Bonferroni-corrected) 0.05 level between the diet of *Physa* shown in Table 1 and either adult *Goniobasis* or *Leptoxis* over 17 riffle diatom species. There was almost no difference in species composition between these three samples and the substrate sample, scraped off the rocks with a scalpel. The only exceptions involved the under-representation of two large diatoms in the snail guts, *Cymbella tumida* (Breb.) and *Synedra rumpens* Kutz. *Synedra rumpens* is a very long, slender species,

Table 1. Abundances of the diatoms collected in seven samples taken in April, 1981, from the Mitchell River, North Carolina.

	Goniobasis adult riffle	*Goniobasis* juvenile riffle	*Leptoxis* juvenile riffle	*Physa* adult riffle	Substrate riffle	Substrate pool	*Goniobasis* adult pool
Achnanthes deflexa	1117	1223	1091	1114	1090	853	900
A. microcephala	41	48	62	43	42	0	0
A. minutissima	1	2	0	1	0	183	141
Amphipleura pellucida	0	0	0	0	0	3	0
Amphora ovalis	1	0	1	0	0	3	3
Cocconeis placentula	34	6	31	37	35	8	9
Cymbella minuta	3	1	4	7	3	6	6
C. tumida	1	2	6	7	21	9	11
Gomphonema angustatum	6	4	9	4	4	6	9
G. parvulum	13	8	16	13	13	10	11
G. clevei	0	0	0	0	0	0	1
Navicula cryptocephala	24	21	25	26	17	78	53
N. decussis	30	38	51	33	31	53	41
N. rhynchocephala	0	0	0	0	0	11	33
Nitzschia acicularis	19	0	24	15	16	4	13
Stauroneis anceps	0	0	0	1	3	3	5
S. phoenicenteron	0	0	0	0	0	1	1
Surirella ovata	0	1	0	1	0	2	1
Synedra fasciculata	21	6	31	25	15	66	67
S. rumpens	135	120	95	113	156	126	90
S. ulna	54	20	52	62	61	75	106
TOTAL	1500	1500	1498	1502	1507	1500	1501

with an average length of 54 micrometres but width of only 3–8 micrometres in the substrate sample. It was under-represented in the gut of *Leptoxis*. *Cymbella tumida* is arguably the largest diatom species collected in this study. Although *Synedra* cells often have greater apical dimensions, *Cymbella* is wide as well as long (average length 51.5 micrometres, width 15.5 micrometres on riffle substrate). *Cymbella* was significantly under-represented in the gut contents of adult *Goniobasis*.

Table I shows that the diet of juvenile *Goniobasis* seems to be somewhat distinct from that of the other snails sampled from the riffle. Juvenile *Goniobasis* guts contained significantly fewer cells of *Cocconeis placentula*, *Nitzschia acicularis* (Kutz.), and *Synedra*, and significantly more of the smaller *Achnanthes deflexa* Reim., than the substrate or the other three snail samples. But our initial impression was that the juvenile *Goniobasis* sample contained a substantially greater proportion of fragmentary diatom frustules, suggesting that food processing was rougher in these snails. This impression was confirmed by the results reported in Table 2. Adult *Goniobasis*, *Leptoxis*, and *Physa* guts contained lower proportions of broken diatoms than the sample obtained with the scalpel blade, in most cases. However, juvenile *Goniobasis* guts contained significantly more fragments of *Cymbella* and *Synedra*, as well as higher proportions of unidentifiable diatom fragments overall.

In addition to grazing a nearly random sample of the diatom species present in the riffle, *Goniobasis* adults seemed to randomly ingest the range of sizes available for each species. Table 3 shows the average apical dimension for the ten most common diatom species collected from the riffle substrate in April. No significant difference was detected between these figures and the mean sizes of the diatoms in the guts of adult *Goniobasis*. This was not the case for *Physa*, *Leptoxis*, or juvenile *Goniobasis*, however. In spite of the fact that no significant difference was detected in the species composition of *Physa* and adult *Goniobasis* diets, *Physa* apparently selected the larger cells from the smaller diatom species (*Achnanthes*) and smaller cells from the larger species (*Synedra*). Table 4 shows similar phenomena in *Leptoxis* and juvenile *Goniobasis*, although not as marked.

The difference between the riffle and pool substrate samples was striking (Table 1). About 10% of the diatom cells collected from the muddy bottom of the shady pool were *Achnanthes minutissima* Kutz., a species apparently so rare in the riffle as to be missed in the rock scrapings entirely, and much higher numbers of *Navicula cryptocephala* Kutz. and *Synedra fasciculata* were also collected in the pool. Four additional diatom species were identified from pool samples, while 1 riffle species was absent. But there was no difference significant at the 0.05 level between the frequencies of any of the 20 diatom species collected on the substrate of the pool and in the guts of adult *Goniobasis* dwelling there. Once again, adult *Goniobasis* seemed to sample the diatom flora randomly, in this case, like a Pasteur pipet.

A great deal of seasonal variation was also apparent in the diet of adult *Goniobasis*. All the shifts in the major components of the diatom flora ingested by *Goniobasis* shown in Table 4 are highly significant with N = 1500. Although it remained the most common diatom species in *Goniobasis* guts, *Achnanthes* became much less common in

Table 2. Proportions of broken diatom frustules (less than half remaining) in counts of 300 identifiable cells. Asterisks mark values different from the substrate at the 0.05 level (Bonferroni corrected).

	Substrate	Adult *Goniobasis*	Juvenile *Goniobasis*	Adult *Physa*	Juvenile *Leptoxis*
Cocconeis	0.52	0.52	0.43	0.32	0.43
Cymbella	0.29	0.86	1.00*	0.36	0.14
Syndra	0.36	0.41	0.63*	0.23	0.25
Unidentifiable to genus	0.25	0.23	0.39*	0.31	0.25

Table 3. Mean and standard deviation (in micrometres) for the apical length of the ten most common diatom species in the riffle substrate sample, and significantly different values obtained from the guts of snails. Dashes designate nonsignificant values. We found no significant difference between substrate and adult *Goniobasis* guts with respect to diatom size.

	Substrate		Adult *Physa*		Juvenile *Leptoxis*		Juvenile *Goniobasis*	
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Synedra ulna	80.3	27.6	49.2	12.5	56.2	18.1	49.5	14.2
S. rumpens	54.0	30.6	32.5	11.4	–	–	32.4	10.1
S. fasciculata	46.4	7.4	32.5	3.5	–	–	32.4	3.5
Nitzschia acicularis	25.6	4.3	–	–	33.5	3.2	(none)	
Cocconeis placentula	23.4	4.6	18.6	1.9	–	–	18.6	4.6
Navicula cryptocephala	22.4	3.0	–	–	–	–	–	–
N. decussis	20.7	2.5	–	–	24.1	2.5	–	–
Gomphonema parvulum	21.0	3.2	–	–	–	–	–	–
Achnanthes deflexa	12.0	3.3	14.9	3.2	15.3	3.3	–	–
A. microcephala	11.8	1.2	12.9	1.6	–	–	–	–

Table 4. Seasonal frequencies of the four most common diatom genera in the guts of adult *G. proxima*, collected from riffle and pool.

	Spring	Summer	Fall	Winter
Achnanthes	0.733	0.950	0.682	0.518
Cymbella	0.007	0.009	0.107	0.031
Gomphonema	0.013	0.011	0.078	0.113
Synedra	0.158	0.012	0.043	0.232

the fall and winter. Increasingly common in the fall and winter were *Gomphonema angustatum* and *G. parvulum* Kutz. Several taxa of large diatoms under-represented in the guts of the snails sampled in spring nevertheless became much more common in fall and winter – *Cymbella tumida*, *Synedra rumpens*, and *Synedra ulna* (Nitz.). One additional diatom species, *Navicula tripunctata* (Mull.), was found rarely in snail guts in both summer and winter.

Discussion

The riffle diatom flora of the Mitchell River at our study locality seems to be typical of rapidly-flowing streams with acidic, nutrient-poor water worldwide (e.g., Douglas, 1958), and has been called the '*Achnanthes*/*Gomphonema*/*Synedra* group' by Round (1973). Round (1964; 1973) observed that these taxa of diatoms are generally sessile, and are thus suited to life on stones in rapidly-flowing water. The motile diatoms (e.g., *Navicula*) are more commonly epipelic, living on the surface of sediments. Thus the striking differences apparent between the diatoms scraped from rocks at midstream and those pipetted from the bottom of a calm, muddy pool at stream's edge are not unexpected. McIntire (1968) found that growth in *Cocconeis placentula* and *Nitzschia acicularis* was stimulated by high current velocity, but that *Achnanthes minutissima* was indifferent to flow rate. *Synedra rumpens* seems to grow better at higher current velocity than *S. ulna* (Steinman and McIntire, 1986). The effects that light, current velocity, depth, and many other environmental variables may have upon diatom floras is reviewed by Blum (1956).

The sample of diatoms obtained from the guts of adult *Goniobasis* grazing over the pool was indistinguishable from the sample obtained from the mud surface by Pasteur pipet. Likewise the sample obtained from the guts of adult *Goniobasis*, *Physa*, and *Leptoxis* grazing of the riffle were

almost indistinguishable from that obtained with a scalpel from rocks. It seems that the diatoms ingested by freshwater snails are primarily a function of relative abundance.

However, the largest diatom species in the riffle sample, *Cymbella tumida*, was significantly under-represented in adult *Goniobasis*, while the unusually long and narrow *Synedra* was under-represented in *Leptoxis* guts. And in most cases, the individual *Synedra* cells ingested tended to be significantly smaller than the average of the cells available. Thus some reduction in snail grazing pressure may result when diatoms grow to an unusually large size.

Interestingly, unusually small diatoms may also escape some grazing pressure. The physically smallest genus of diatoms, *Achnanthes*, was by far the most common group in all samples, including riffle substrate where snails densities were high. And in some cases, the mean size of the *Achnanthes* cells ingested by snails was significantly larger than the mean size of those available. *Achnanthes* was so much smaller than the other diatom taxa that escape by the smaller cells did not alter its proportion in snail diets, however.

We noticed several other cases of size selection in particular diatom species that are harder to interpret. *Leptoxis* seemed to selectively ingest larger *Navicula* cells, and *Physa* and juvenile *Goniobasis* seemed to ingest smaller *Cocconeis placentula*. One might speculate that these phenomena relate to some aspects of the biology of the snail or the diatom. We did not see any evidence of the under-representation of *Cocconeis* in snail diets reported by previous workers (Patrick, 1970; Hunter, 1980; Kesler, 1981), but perhaps the adhesive abilities of this diatom make small cells more vulnerable to grazing by some snails.

Our results regarding juvenile *Goniobasis* must be viewed in light of the significantly rougher processing apparently given to diatom frustules by these snails. The striking absence of *Nitzschia acicularis* from juvenile *Goniobasis* samples, as well as the lower counts of *Synedra ulna* and *S. fascicularis*, were probably due to breakage. *Nitzschia* forms very long, slender, almost filamentous frustules. If broken, they would appear to be unidentifiable fibers or setae. Perhaps smaller crystalline styles have greater grinding ability. The lower frequency of *Cocconeis* in juvenile *Goniobasis* does not seem to be due to processing, however. None of the snails seemed to be significantly rougher on *Cocconeis* frustules than a scalpel blade.

The way in which radular ribbons may be employed (Hickman & Morris, 1985) is a source of variation we have not considered. But Dillon (1981; 1987) has suggested that radular similarity may indirectly estimate dietary similarity in freshwater snails. Thus we were surprised that radular morphology did not seem to play a more important role in the diatoms ingested. The species composition in the gut of *Physa* was indistinguishable from that of adult *Goniobasis* or juvenile *Leptoxis*, two snails with radulae differing in nearly every respect from that of *Physa*. And if any snail has a distinctive diet, it would be juvenile *Goniobasis*, with a radula indistinguishable from that of juvenile *Leptoxis*. The greater uniformity of cusp size in *Physa* may account for a greater uniformity in the sizes of the diatoms it ingests, but this would not seem to be an adaptation to minimize competition with co-occurring species of snails. In fact, to the extent that diatoms are a limiting resource to these snail populations, competition between *Goniobasis*, *Leptoxis*, and *Physa* would be intense. But it should be noted that there are doubtless other components to the diets of these snails, and that these three species are rarely found together.

The diatoms ingested by freshwater snails generally resembled samples taken by humans using conventional techniques. Regardless of the type of snail collected, most diatom species available were represented in similar proportions in snail gut and scapings. And if one considers presence/absence of individual diatom species only, as in the simple matching coefficient of Dillon (1984), snail samples seemed to match the natural population very closely. Pulmonates, prosobranchs, adult snails and juvenile all ingested at least a few cells of all diatom species present. The only significant absence shown in Table 1, over five snail samples of 21 diatom

species in two environments, was the apparent absence of *N. acicularis* from juvenile *Goniobasis* guts, due almost certainly to breakage.

In July, 1980, Dillon (1982; 1984) collected *Goniobasis* from 24 additional creeks spread from Danville, Virginia, to Bristol, Tennessee, in four major drainages. By far the most common diatom species in guts, at least 15% at all localities, was *Achnanthes defexa*. This species and the next most common species, *A. minutissima*, comprised an average of 74% of the diatom cells identified at each locality. But the species richness was high. Including the summer Mitchell River locality reported here, a total of 150 diatom species were identified, representing 23 genera. There is reason to believe that this species richness accurately reflects the diatom flora in the creeks of this region. Similarly, the temporal variability found in *Goniobasis* gut samples at the Mitchell River probably also reflects the actual dynamics of the diatom flora. Striking seasonal changes in diatom floras have been documented by many authors (Douglas, 1958; Blum, 1956; Round, 1964).

In some habitats it may be easier to collect snails than to collect diatoms. This might be the case in deep or turbid water, for example, or on a submerged rock surface. If one keeps in mind that frustule sizes and proportions of larger diatom species may be skewed, a survey of snail gut contents in these situations may be recommended.

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