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Abstract

The southern Appalachian Mountains are home to the greatest diversity of Blephariceridae (Dipter) in North America, with 13 Blepharicera Macquart species inhabiting the region. Sympatric Blepharicera species seem to occupy a common ecological niche, in contradiction to the competitive exclusion principle. Instar IV Blepharicera larvae were studied to determine whether dietary differences facilitate coexistence of sympatric species. Diatom assemblages of Blepharicera diets, total diatom biovolume ingested, and similarity between diatom assemblages of larval diets and the forage base were examined. Dietary characteristics were compared among Blepharicera species within and between discrete microhabitats at 3 sites in southern Appalachia. Data showed broad dietary overlap among species that co-occurred in the same microhabitat and strong microhabitat effects on larval dietary assemblages. In addition, several species ingested disproportionately greater biovolumes of small, adnate and prostrate diatom species compared to their availability on the substratum. Sym- patric Blepharicera species may not partition food resources where spatial overlap is most acute.

Keywords

Blephariceridae, net-winged midges, niche, grazer, diatoms, southern Appalachian mountains

Disciplines

Behavior and Ethology | Ecology and Evolutionary Biology | Entomology

Comments

Niche overlap of sympatric *Blepharicera* larvae (Diptera:Blephariceridae) from the southern Appalachian Mountains

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Abstract. The southern Appalachian Mountains are home to the greatest diversity of Blephariceridae (Diptera) in North America, with 13 *Blepharicera* Macquart species inhabiting the region. Sympatric *Blepharicera* species seem to occupy a common ecological niche, in contradiction to the competitive exclusion principle. Instar IV *Blepharicera* larvae were studied to determine whether dietary differences facilitate coexistence of sympatric species. Diatom assemblages of *Blepharicera* diets, total diatom biovolume ingested, and similarity between diatom assemblages of larval diets and the forage base were examined. Dietary characteristics were compared among *Blepharicera* species within and between discrete microhabitats at 3 sites in southern Appalachia. Data showed broad dietary overlap among species that co-occurred in the same microhabitat and strong microhabitat effects on larval dietary assemblages. In addition, several species ingested disproportionately greater biovolumes of small, adnate and prostrate diatom species compared to their availability on the substratum. Sympatric *Blepharicera* species may not partition food resources where spatial overlap is most acute.

Key words: Blephariceridae, net-winged midges, niche, grazer, diatoms, southern Appalachian mountains.

The competitive exclusion principle states that 2 species of sufficiently large population size cannot occupy the same ecological niche indefinitely (Gause 1934, Hutchinson 1957, Hardin 1960). The exclusion principle predicts that suites of closely related sympatric species will have divergent ecological characteristics that allow their coexistence (Hutchinson 1957). In the absence of experimental or observational evidence of resource partitioning among sympatric species, one is advised either to look harder or to consider the possibility that resources are not limiting (Hutchinson 1957). Ecological and reproductive isolation are common among sympatric stream invertebrates, and have been revealed through differences in life-history patterns (Wallace and Anderson 1996 and references therein), longitudinal distribution (Hildrew and Edington 1979), microdistribution (Anderson and Bourne 1974, Hildrew and Edington 1979, Teague et al. 1985), thermal optima (Hildrew and Edington 1979, Vannote and Sweeney 1980, Sweeney and Vannote 1981), and dietary habits (Cummins and Merritt 1996 and references therein). Net-winged midge larvae (Diptera: Blephariceridae) are rheophilic specialists that inhabit cascades, waterfalls, and currents that can exceed 400 cm/s (Craig 1966). The southern Appalachian Mountains are home to the greatest diversity of Blephariceridae in North America, with 13 *Blepharicera* Macquart species inhabiting the region (Courtney 2000). Despite relatively narrow habitat requirements, local sympatry of ≥3 congeneric species is common in streams throughout southern Appalachia (Courtney 2000).

Spatial isolation (Kitakami 1950, Zwick 1977, 1980) and temporal isolation (Zwick 1977, Courtney 1991, Johns 1996) have been reported for sympatric Blephariceridae, but no studies have explored dietary partitioning among these organisms. In southern Appalachia, potential overlap in exploitation of resources is exacerbated by structural homogeneity of immature *Blepharicera*. This homogeneity presumably reflects a common need for certain structural adaptations, given the group's unusual rheophilic restrictions, and is particularly evident in the ex-

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tremely conservative mouthpart structure observed across most genera of Blephariceridae, including *Blepharicera* (Courtney 2000).

Blepharicerid larvae use specialized mouthparts (Fig. 1A) to graze periphytic films from submerged substrata. Based on meticulous observations of larvae in laboratory aquaria, Tonnoir (1930) was first to document the blepharicerid feeding mechanism, describing these larvae as ''grazing like cattle in a paddock''. Robust mandibles move back and forth, scraping the substratum to dislodge epilithic algae, mostly diatoms (Tonnoir 1930, Arens 1989, Courtney 1990). Dissected mandibles from a recently ecdysed larva (Fig. 1B) and a mature larva (Fig. 1C) demonstrate the abrasive effect of this behavior on larval mouthparts. As mandibles are extended forward, maxillae (Fig. 1A, mxl) are simultaneously pressed against the substratum. When mandibles are retracted, maxillae are drawn medially, sweeping dislodged food particles into the cibarium (Tonnoir 1930, Courtney 1990). A large, padlike labium (Fig. 1A, lbm) is thought to prevent posterior food escape (Courtney 1990).

Our primary goal was to determine whether dietary differences facilitate coexistence of sympatric *Blepharicera* species at 3 sites in the southern Appalachian Mountains. We examined diets of several species of instar IV *Blepharicera* larvae. We assessed diatom assemblages of *Blepharicera* diets, estimated total diatom biovolume ingested by *Blepharicera*, and compared diatom assemblages of *Blepharicera* diets to assemblages of the forage base. We compared dietary characteristics among *Blepharicera* species within and between discrete microhabitats at each site.

Methods

Study sites

We chose 3 sites in the southern Appalachian Mountains based on habitat characteristics and knowledge of *Blepharicera* faunal diversity and phenology. Diversity, season of larval growth, and habitat characteristics of *Blepharicera* fauna at each site are summarized in Table 1.

Brasstown Falls.—Brasstown Creek (lat 34°42′N, long 83°18′W), a 3rd-order stream in Sumter National Forest, northwestern South Carolina, is part of the Savannah River basin. The reach of Brasstown Creek that we sampled, Brasstown

Falls, is ~10 m in width and is characterized by a cascade and 2 waterfalls. Brasstown Falls is the most shaded of the 3 sites, with rhododendron (*Rhododendron* sp.) and mountain laurel (*Kalmia latifolia* L.) dominating riparian vegetation and overhanging cascades and waterfalls; in addition, various pine (*Pinus* spp.) and hardwood species are scattered throughout the riparian zone.

Cataloochee Creek.—The 2nd site, Cataloochee Creek (lat 35°40′N, long 83°04′W), is a 4th-order stream in the Tennessee River basin, draining the southeast sector of Great Smoky Mountains National Park, North Carolina. At our sample site, Cataloochee Creek is ~10 m in width, moderately shaded, and surrounded predominantly by a mixture of eastern white pine (*Pinus strobus* L.) and cove hardwoods (hemlock, *Tsuga caroliniana* (Endl.) Carr and American beech, *Fagus grandifolia* Ehrhart).

Chattooga River.—The 3rd site, Chattooga River (lat 34°48′N, long 83°18′W), is a 5th-order stream that forms the boundary between extreme northeastern Georgia and northwestern South Carolina. Estimated channel width at our sampling site is 40 m. The Chattooga, also in the Savannah River basin, is a National Wild and Scenic River—west and east banks are managed by Chattahoochee and Sumter National Forests, respectively. The Chattooga supports the highest known blepharicerid diversity of any stream sampled to date (Table 1). Chattooga River is least shaded of the 3 sites, its riparian canopy consisting primarily of pines (eastern white pine; short leaf pine, *Pinus echinata* Miller, Gard.; and Virginia pine, *Pinus virginiana* Miller, Gard.), with intermittent hardwoods. The riparian understory consists primarily of rhododendron, mountain laurel, and various herbaceous species.

Study design

Our primary interest was to determine whether *Blepharicera* larvae that come in contact with each other consume the same food. We expected larval species and microhabitat to be important determinants of *Blepharicera* diets; therefore, we designated microhabitats at each site and assessed diets of *Blepharicera* species from them. Dietary assessments and subsequent analyses focused on larval groups (sums of larval conspecifics from a microhabitat). Microhab-
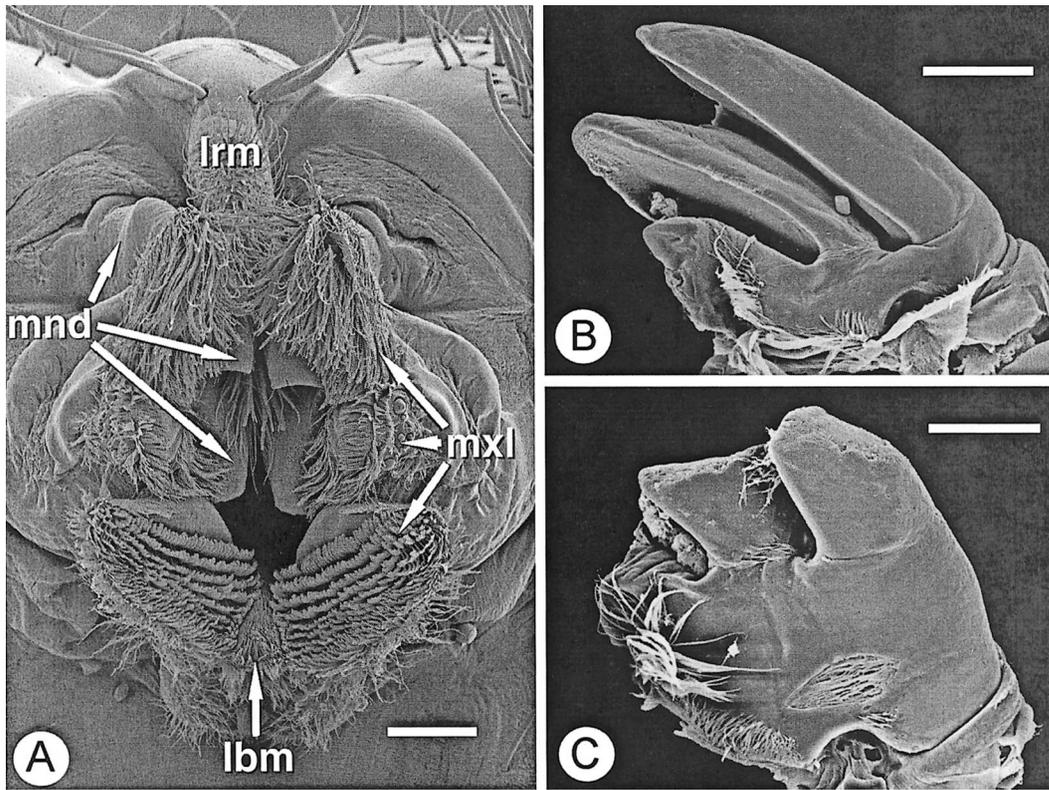
FIG. 1. Scanning electron micrographs of Blephariceridae mouthparts. Scale bar = 50 μm. A.—*Blepharicera cherokea* mouthparts: lrm = labrum, mxl = maxillae, lbm = labium, mnd = mandible. B,C.—Blephariceridae mandibles showing lack of wear in a recently ecdysed larva (B) and worn mandibles caused by scraping in a mature larva (C).

itat characteristics and number of larvae per larval group are summarized in Table 2. We expected diets of congeneric species to be most disparate where spatial overlap was greatest (i.e., within a microhabitat); such within-microhabitat differences between species would suggest a *species effect* on diets. Significant dietary differences between *conspecific* larvae that occupied >1 microhabitat per site would suggest a *microhabitat effect* on diets. We focussed on within-site comparisons because between-site comparisons were confounded by qualitative differences in *Blepharicera* fauna (Table 1) and diatom flora (see below) at different sites.

Three distinct microhabitats were identified and sampled at Brasstown Falls (Table 2). The 1st was emergent bedrock exposed to the persistent crash of falling water; this *crash zone* was at the base of Brasstown's lower falls. The 2nd microhabitat was a *hygropetric zone* adjacent to

the cascade. The 3rd microhabitat was a *cascade* characterized by continuous, rapidly flowing water of ~5 cm depth. Two microhabitats were identified and sampled at Cataloochee Creek (Table 2). The 1st was submerged cobble from a *fast riffle* where mainstream current velocity was ~232 cm/s. The 2nd was submerged cobble from a *slow riffle* where mainstream current velocity was ~90 cm/s. Two microhabitats were identified and sampled at Chattooga River (Table 2). The 1st was a *bedrock chute* where current velocity was ~250 cm/s. The 2nd was submerged cobble from a *slow riffle* where mainstream current velocity was ~95 cm/s.

Field methods

All samples were collected in mid-May 1998, when greatest number of *Blepharicera* species are apt to be present (Table 1). Each site was sam-

TABLE 1. Diversity and generalized patterns of ecological isolation of sympatric *Blepharicera* from Brasstown Falls (BF), Cataloochee Creek (CC), and Chattooga River (CR). Data are based on collections from 1990–1999. Species code: NU = not used. Relative abundance: COM = common, UNC = uncommon, RAR = rare, – = absent. Current regime: L = low, M = medium, H = high.

| Species | Species code | Relative abundance | | | Season of larval growth | Current regime |
		BF	CC	CR		
Blepharicera coweetae Hogue & Georgian	NU	RAR	COM	COM	Winter	H
B. magna Courtney	NU	–	COM	UNC	Winter	H
B. williamsae Alexander	NU	COM	COM	RAR	Winter	H
B. capitata Loew	NU	–	–	UNC	Early spring	L
B. appalachiae Hogue & Georgian	*app*	–	COM	COM	Spring	L
B. cherokea Hogue	*che*	COM	COM	UNC	Spring	H
B. corniculata Courtney	*cor*	–	–	UNC	Spring	H
B. tuberosa Courtney	*tub*	–	COM	–	Spring	H
B. separata Alexander	*sep*	RAR	UNC	COM	Early summer	L
B. chattooga Courtney	NU	–	–	COM	Summer	L
B. diminutiva Hogue	*dim*	COM	–	RAR	Summer[a]	Hygropetric
B. similans Johannsen	*sim*	COM	COM	COM	Summer–autumn[a]	M

[a] Possibly multivoltine

pled midday (1300–1700 h EST) to eliminate the potential complication of fluctuating diel feeding rates. Because blepharicerid distribution within streams is often patchy and nonrandom, sampling was based primarily on presence of larvae and was, therefore, nonrandom. Our samples, in essence, are representative of ideal blepharicerid habitat. Within a microhabitat, rocks were randomly selected and larvae were removed individually with forceps and preserved in 6:3:1 (95% ethanol:collection water: 10% formalin) solution. Mainstream current velocity was measured directly above each rock sampled when appropriate. These measurements were then averaged over a microhabitat, with the range not exceeding 20 cm/s. Although we were interested only in diets of instar IV larvae, all larvae beyond instar II were col-

TABLE 2. Microhabitat characteristics and numbers of *Blepharicera* larvae from each site. NA = not available. Species abbreviations as in Table 1.

Site	Substratum	Microhabitat	Current velocity (cm/s)	Species	Number of larvae
Brasstown Falls	Bedrock	Crash zone	NA	*B. dim*	9
				B. sim	11
	Bedrock	Hygropetric zone	NA	*B. dim*	14
				B. sim	9
	Bedrock	Cascade	NA	*B. sim*	18
Cataloochee Creek	Cobble	Fast riffle	232	*B. app*	4
				B. che	7
				B. sim	20
				B. tub	11
	Cobble	Slow riffle	90	*B. app*	12
				B. sim	13
Chattooga River	Bedrock	Bedrock chute	250	*B. cor*	13
				B. sim	9
	Cobble	Slow riffle	95	*B. sep*	20

lected (because of small size, collection of instars I is possible only by thoroughly washing rocks). This method minimized problems with field identification of larvae and prevented sampling bias toward large individuals. After removal of larvae, ambient (source) diatoms were removed with a toothbrush and preserved in the 6:3:1 solution. Diatoms were collected from areas that varied with larval distribution on substrata. This collection method prevented estimates of cell density, but it was intended to minimize the impact of potentially aberrant diatom patches outside the immediate larval grazing pasture on estimation of source assemblage structure. All larval and diatom collections consisted of pooled material from 2 or 3 rocks or a single piece of bedrock (e.g., Brasstown Falls and Chattooga River chute). Bedrock sampling required that water be shunted away from the collection area, which was accomplished with a modified polyvinylchloride (PVC) pipe fitted with a soft, pliable collar.

Laboratory assessments

Instar IV larvae consume considerably more food than earlier instars (AJA, unpublished data), a finding consistent with reports of maximum production of *B. williamsae* at the end of its larval period (Georgian and Wallace 1983). This attribute is shared by other insect groups (Waldbauer 1968). Furthermore, larvae discontinue feeding and empty their guts prior to instar–instar molts and larva–pupa molts (AJA, unpublished data); therefore, we examined only midstage, instar IV larvae. Prior to dissection, body length and head-capsule width of each larva were recorded. The entire gut was then dissected out under a stereo microscope. Gut contents were transferred to a coverslip with ~10 μL of 30% hydrogen peroxide, and the material was mechanically spread and macerated, allowed to dry, and permanently slide-mounted with Naphrax. Source diatoms were acid-cleaned according to Patrick and Reimer (1966), air dried onto a coverslip, and slide-mounted with Naphrax. All samples were examined at 600× with a Nikon E800 compound microscope. Full transects were examined until ≥1000 diatom valves per sample had been identified and counted. If a gut sample consisted of <1000 diatom valves, the entire slide was counted. Valves rather than frustules were counted because of

potential differences in the propensity of diatom taxa to separate from an intact frustule into valves. At least ½ of a diatom valve, including the central nodule, had to be present to be included in counts. Slides also were scanned to record rare taxa. Diatoms were identified using standard taxonomic references (Hustedt 1930, Patrick and Reimer 1966, 1975, Krammer and Lange-Bertalot 1991a, 1991b, 1997a, 1997b) and various floristic studies of diatom species from the southeastern United States (Camburn and Lowe 1978, Kociolek 1982, Lowe and Kociolek 1984). Diatom images of common taxa are available in Alverson (2000).

Data analysis

Raw counts were translated into absolute biovolumes with estimates generated in BIOVOL (D. B. Kirschtel. 1996. BIOVOL, version 2.1. Available from: http://www.uvm.edu/~dkirscht/biovol.html). Critical measurements were taken for 20 cells each for common taxa and as many cells as possible for rare taxa, and the average of these measurements was used for biovolume calculations. Data were standardized by conversion of absolute biovolumes to proportions of the total (i.e., relative biovolumes). Diatom taxa with an average of ≥2% relative biovolume of ≥1 larval group or source diatom sample were included in statistical analyses. Each site was analyzed independently. For each site, relative biovolume data for common diatom taxa were used to generate dissimilarity (distance) matrices with the Bray–Curtis metric (Bray and Curtis 1957). The Bray–Curtis metric weights abundant dietary attributes more heavily than rare ones, is insensitive to joint absences, and generally is regarded as a stable distance measure (Field et al. 1982, Faith et al. 1987, Boyle et al. 1990).

Ordination.—Gut and source samples were ordinated with nonmetric multidimensional scaling (NMDS, Kruskal and Wish 1978) to evaluate whether diatom assemblages of larval guts differed among larval groups and from the corresponding source sample. NMDS requires few assumptions, allows user-defined distance measures, and is useful when one insists only on preserving a monotonic relationship between biological distance and plot distance. Using any triangular distance matrix, pairwise sample distances are rank-ordered from lowest to highest

(or vice versa) and, through an iterative procedure, samples are ordinated in low-dimensional space on the basis of rank similarity alone (Kenkel and Orlóci 1986, Clarke 1993). The stress coefficient measures disagreement between the distance matrix and ordination plot. Stress values increase as sample number increases and number of plot dimensions decreases; in general, stress values <0.1 are considered interpretable (Clarke 1993). We used ordinations based on pairwise sample distances calculated using the Bray–Curtis metric on untransformed data. NMDS procedures were run with the ''medium'' setting of autopilot mode in PC-ORD (B. McCune and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon). In this mode, ≤200 iterations are performed for each of 15 runs of the procedure, and each procedure has a random starting configuration. Solutions were terminated after 200 runs or when the SD of stress divided by the number of iterations was <0.0001. For each site, the solution with the least number of dimensions and a corresponding stress coefficient <0.1 was chosen. Scores for species ordinations were generated with a weighted-averaging step and thus have no stress coefficient.

Diet overlap.—Mantel permutation procedures (MPP, Mantel 1967) were used to explore differences in dietary assemblages among larval groups. MPPs also were used to evaluate whether microhabitats could be distinguished on the basis of collective larval gut samples. These interhabitat comparisons were done by grouping all larval samples from each habitat and then running MPP on designated habitat groups. MPPs test the null hypothesis of no correlation between 2 distance matrices. The null hypothesis of our study was one of no difference in dietary assemblages between larval groups. For each test, a Bray–Curtis distance matrix was compared against a design matrix (Sokal and Rohlf 1995, Legendre and Legendre 1998). The design matrix had 0s for all within-group distances and 1s for all between-group distances; in essence, the design matrix depicted the hypothesis that between-group differences were greater than within-group differences (Sokal and Rohlf 1995, Legendre and Legendre 1998). The procedure unfolds the 2 distance matrices and computes the Mantel statistic (z_M), which is the sum of crossproducts of unstan-dardized values in the unfolded matrices (Mantel 1967). The Mantel statistic is tested using a permutation procedure in which objects in 1 of the original distance matrices are permuted, and z_M is recalculated. The latter is repeated to establish a distribution for z_M. For our study, MPPs were performed with 9999 randomized runs to obtain the distribution for z_M. Using MPP with a design matrix is analogous to performing a nonparametric multivariate analysis of variance (Sokal et al. 1993, Legendre and Legendre 1998).

Total diatom biovolume.—Total diatom biovolume ingested per individual was estimated and compared among larval groups. Total biovolume was estimated by considering number of diatom valves enumerated, estimated biovolume per taxon, area examined, and total slide area. A 1-factor analysis of variance (ANOVA) was used to assess intra- and interhabitat differences of log-transformed total biovolume estimates among larval groups. All ANOVAs were run with the general linear models procedure (proc GLM) in SAS (version 6.12, SAS Institute, Inc., Cary, North Carolina). Preplanned multiple comparisons were made with 2 sample *t*-tests, with the least squares means (LSMEANS) statement in the GLM procedure. For MPP and ANOVAs, the sequential-Bonferroni method was used to maintain an experimentwise Type I error rate of α = 0.05 (Holm 1979).

Results

Growth habit, estimated biovolume, and distribution of common diatom species among study sites are summarized in Table 3. Larval dietary and source diatom assemblages were characterized by 27 common diatom taxa, 12 of which occurred at all 3 sites and 10 of which were unique to 1 site. Mean diatom biovolume ranged from 51 μm^3/frustule (*Achnanthidium minutissimum*) to 4902 μm^3/frustule (*Frustulia rhomboides* v. *amphipleuroides*).

Brasstown Falls

Ordination.—A 3-dimensional ordination was the only NMDS solution with a stress value <0.1. For clarity, the sample ordination was displayed in 3 panels (Fig. 2A–C), and the number of diatom species was reduced by displaying

TABLE 3. Characteristics of the 27 most common diatom taxa from substrata and *Blepharicera* diets at Brasstown Falls (BF), Cataloochee Creek (CC), and Chattooga River (CR).

Species	Species code	Growth habit	Estimated biovolume (μm^3/cell)	Presence/absence in samples		
				BF	CC	CR
Diatoma mesodon (Ehr.) Kütz.	DIME	Zig-zag colonies	694	−	+	−
Diatoma vulgaris Bory	DIVU	Zig-zag colonies	2826	+	−	−
Synedra rumpens (Kütz.)	SYRU	Rosette-forming	196	+	+	+
Synedra cf. *ulna*	SYUL	Rosette-forming	1124	+	+	+
Fragilaria vaucheriae (Kütz.) Peters.	FRVA	Chain-forming	239	+	+	+
Cocconeis placetula v. *lineata* (Ehr.) V.H.	COPL	Adnate	351	+	+	+
Achnanthes deflexa v. *alpestris* Lowe & Kociolek	ACDF	Adnate	94	−	+	+
Achnanthes subhudsonis v. *kraeusellii* Choln.	ACSH	Adnate	83	+	+	−
Achnanthes sp. #5	ACH5	Adnate?	69	+	−	−
Planothidium lanceolatum (Bréb) Round & Bukhtiya-rova	PLLA	Adnate	188	+	+	+
Achnanthidium minutissimum (Kütz.) Czarnecki	ACMI	Adnate	51	+	+	+
Eunotia spp.	EUNO	Unattached, chain-forming	510	+	+	+
Navicula angusta Grun.	NAAN	Motile	921	−	+	+
Navicula cryptotenella Lange-Bertalot	NACT	Motile	362	+	+	+
Navicula lanceolata (Ag.) Kütz.	NALA	Motile	1631	+	−	−
Navicula tripuncta (O.F. Müll.) Bory	NATR	Motile	1357	+	−	−
Frustulia rhomboides v. *amphipleuroides* (Grun.) Cl.	FRAM	Mucilagenous tube-/mat-forming	4902	−	+	+
Frustulia rhomboides v. *capitata* (A. Mayer) Patr.	FRCA	Mucilagenous tube-/mat-forming	1367	−	−	+
Pinnularia termitinia (Ehr.) Patr.	PITE	Unattached, motile	978	−	−	+
Reimeria sinuata (Greg.) Kociolek & Stoermer	RESI	Short stalk-/pad-forming	325	+	+	−
Encyonema silesiacum (Bleisch in Rabenhorst) D.G. Mann	ENSI	Mucilagenous tube-/mat-forming	157	+	+	+
Gomphonema parvulum (Kütz.) Kütz.	GOPA	Pedunculate	237	+	+	+
Gomphonema subclavatum (Grun.) Grun.	GOSU	Pedunculate	291	+	+	+
Gomphonema sp. #1	GOM1	Pedunculate?	60	+	−	−
Gomphonema sp. #5	GOM5	Pedunculate?	62	−	+	−
Epithemia adnata (Kütz.) Bréb	EPAD	Adnate	4733	+	−	−
Nitzschia spp.	NITZ	Motile	557	+	+	+

only those that comprised ≥3% average total biovolume of ≥1 group (Fig. 2D).

In the crash zone, substantial biovolumes of *Synedra* cf. *ulna*, *Epithemia adnata*, and the small, adnate species *Achnanthidium minutissimum* characterized larval diets (Fig. 2A,D, Table 3). Dietary assemblages of larvae from the crash zone were distinguished from dietary assem-
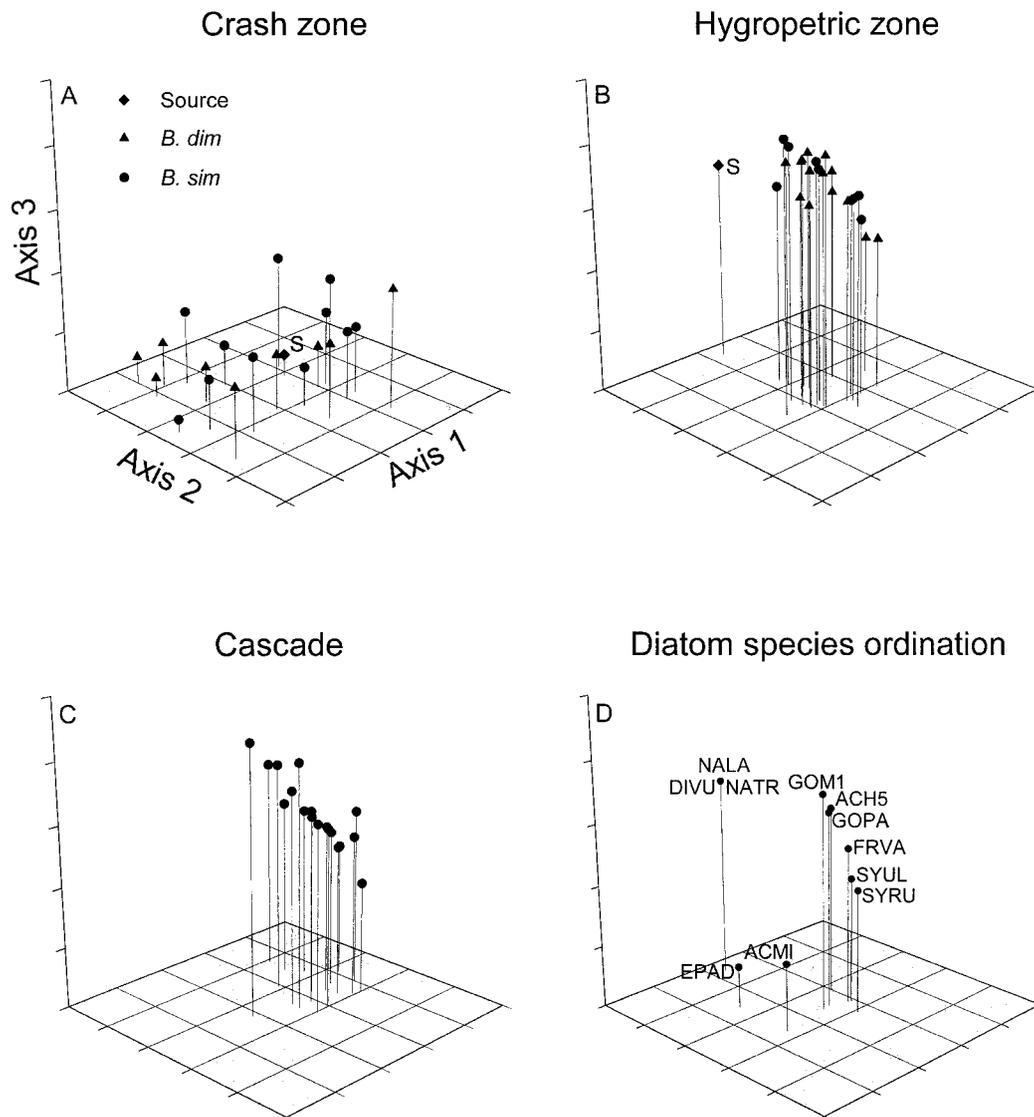
Crash zone

Hygropetric zone

Cascade

Diatom species ordination

FIG. 2. Three-dimensional nonmetric multidimensional scaling plot of Bray–Curtis distances among larval gut and source (S) diatom samples from the crash zone (A), hygropetric zone (B), and cascade (C) at Brasstown Falls, South Carolina. Stress = 0.088. D.—Ordination of common diatom species from *Blepharicera* diets and source diatom samples at Brasstown Falls. Abbreviations of *Blepharicera* as in Table 1, of diatoms as in Table 3.

blages of hygropetric zone and cascade larvae along axes 2 and 3 in ordination space (Fig. 2A–C). *Blepharicera* from the crash zone ingested disproportionately large biovolumes of *A. minutissimum* compared to its availability on the substratum (Fig. 2A,D).

Dietary assemblages of hygropetric zone and cascade larvae overlapped broadly in ordination space, despite subtle displacement along axes 1

and 3 (Fig. 2B,C). In the hygropetric zone, *Blepharicera* primarily ingested *Gomphonema* sp. #1 and *Fragilaria vaucheriae* (Fig. 2B,D). Larval dietary assemblages consisted of disproportionately greater biovolumes of *Gomphonema* sp. #1 compared to its availability on the substratum; in addition, 3 large diatoms (*Diatoma vulgaris, Navicula lanceolata,* and *N. tripunctata*) were numerically abundant on the substratum and ab-

Table 4. Intra- and interhabitat pairwise diet comparisons (p-values) among larval groups of *Blepharicera* at Brasstown Falls, South Carolina, using Mantel permutation procedures. Abbreviations as in Table 1. * = significant after sequential-Bonferroni correction for multiple comparisons (α = 0.05).

| | | Crash zone | | Hygropetric zone | | Cascade |
		B. dim	B. sim	B. dim	B. sim	B. sim
Crash zone	B. dim	–	0.34	0.0001*	0.0001*	0.0001*
	B. sim	–	–	0.0001*	0.0001*	0.0001*
Hygropetric zone	B. dim	–	–	–	0.36	0.007*
	B. sim	–	–	–	–	0.005*

sent from larval diets (Fig. 2B,D). In the cascade, *B. similans* ingested comparable biovolumes of *Gomphonema* sp. #1, *Achnanthes* sp. #5, *F. vaucheriae*, and *S.* cf. *ulna* (Fig. 2C,D). The diatom source sample from the cascade primarily consisted of unidentified bryophytes and too few diatoms to adequately estimate assemblage structure.

Diatom assemblages in guts of *B. diminutiva* and *B. similans* that co-occurred within the crash zone and hygropetric zone were indistinguishable, which resulted in broad overlap of those samples in ordination space (Fig. 2B,C).

MPP.—Dietary differences displayed in ordination plots usually were confirmed by MPP. Collectively, crash-zone samples were significantly different from hygropetric samples (MPP, $p < 0.0001$) and cascade samples (MPP, $p < 0.0001$). The collective hygropetric samples were significantly different from collective cascade samples, despite overlap in ordination space (MPP, $p < 0.0002$). In addition, significant pairwise dietary differences were detected between larvae that occupied different microhabitats; however, no significant pairwise dietary differences were detected between congeners that shared a microhabitat (Table 4).

Total diatom ingestion.—Total diatom ingestion (biovolume) was greatest for *B. similans* from the crash zone, which reflected the abundance of the large diatom *E. adnata* in their diet (Fig. 3A, Table 3). In contrast, *B. similans* from the cascade ingested the lowest total diatom biovolume (Fig. 3A). Total diatom ingestion by *B. similans* was significantly greater than that of *B. diminutiva* where the 2 species co-occurred within the crash zone, although no difference was detected between the 2 species in the hygropetric zone (Fig. 3A).

Cataloochee Creek

Ordination.—NMDS generated a 2-dimensional ordination with stress value <0.1 (Fig. 4). Dietary assemblages of larvae from fast and slow riffles were distinguished along axis 1 in ordination space (Fig. 4A). In the fast riffle, larvae primarily ingested *S.* cf. *ulna*, *Achnanthes deflexa* v. *alpestris*, and *Cocconeis placentula* v. *lineata* (Fig. 4A,B). In the slow riffle, larvae ingested *S.* cf. *ulna* almost exclusively (Fig. 4A,B). Diatom assemblages of *Blepharicera* diets from fast and slow riffles closely resembled diatom assemblages from substrata (Fig. 4A). Source diatom assemblages showed little variation between the 2 microhabitats, each being dominated by *S.* cf. *ulna* (Fig. 4A,B).

MPP.—No significant difference in larval dietary assemblages was detected between fast and slow riffles (MPP, $p = 0.48$). A greater proportion of *A. deflexa* v. *alpestris* in the diet of *B. cherokea* from the fast riffle made those samples somewhat distinguishable from other larval groups (Table 5; Fig. 4A,B). No significant dietary differences were detected among *Blepharicera* species that co-occurred in the fast riffle, despite acute spatial overlap (Table 5). Also, no significant dietary difference between *B. appalachiae* and *B. similans* that co-occurred in the slow riffle was detected (Table 5).

Total diatom ingestion.—*Blepharicera* larvae from the fast riffle ingested significantly greater diatom biovolumes compared to congeners from the slow riffle (Fig. 3B). *Blepharicera tuberosa* from the fast riffle consumed significantly greater biovolumes than all other larval groups at Cataloochee Creek (Fig. 3B). Total diatom ingestion was significantly different between *B. appalachiae* and *B. similans* that co-occurred in
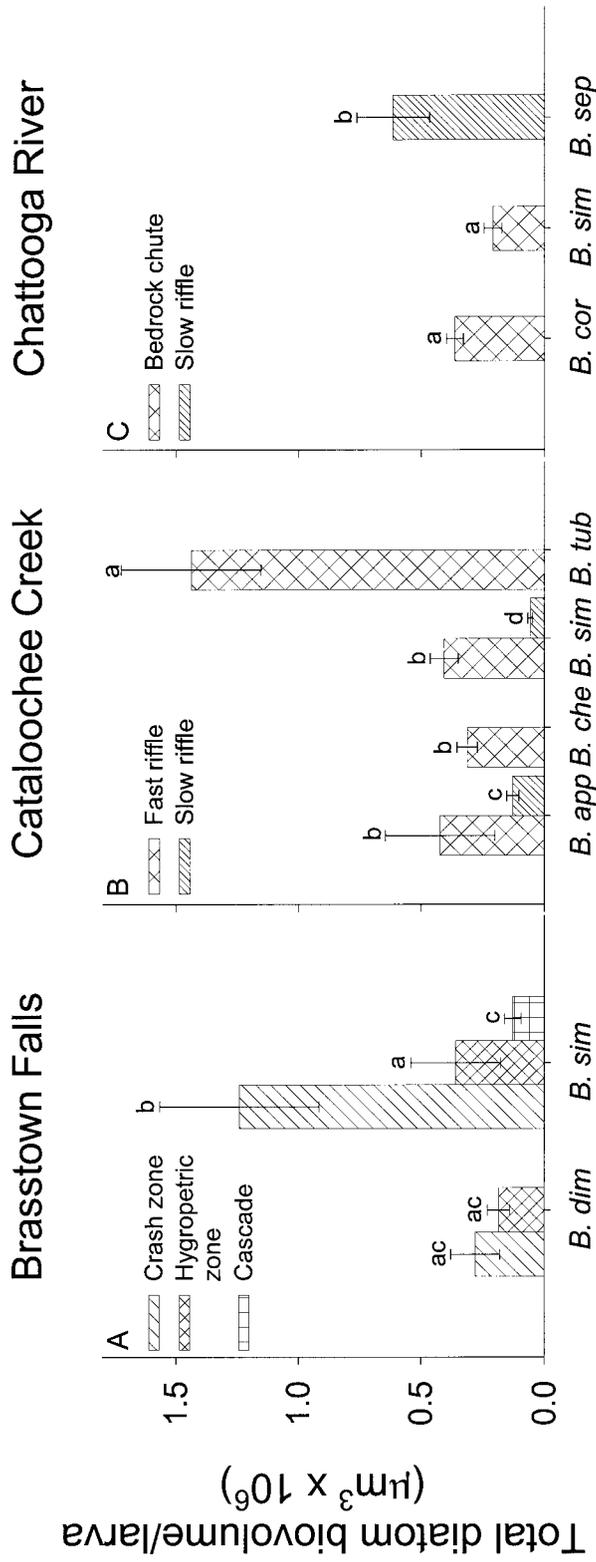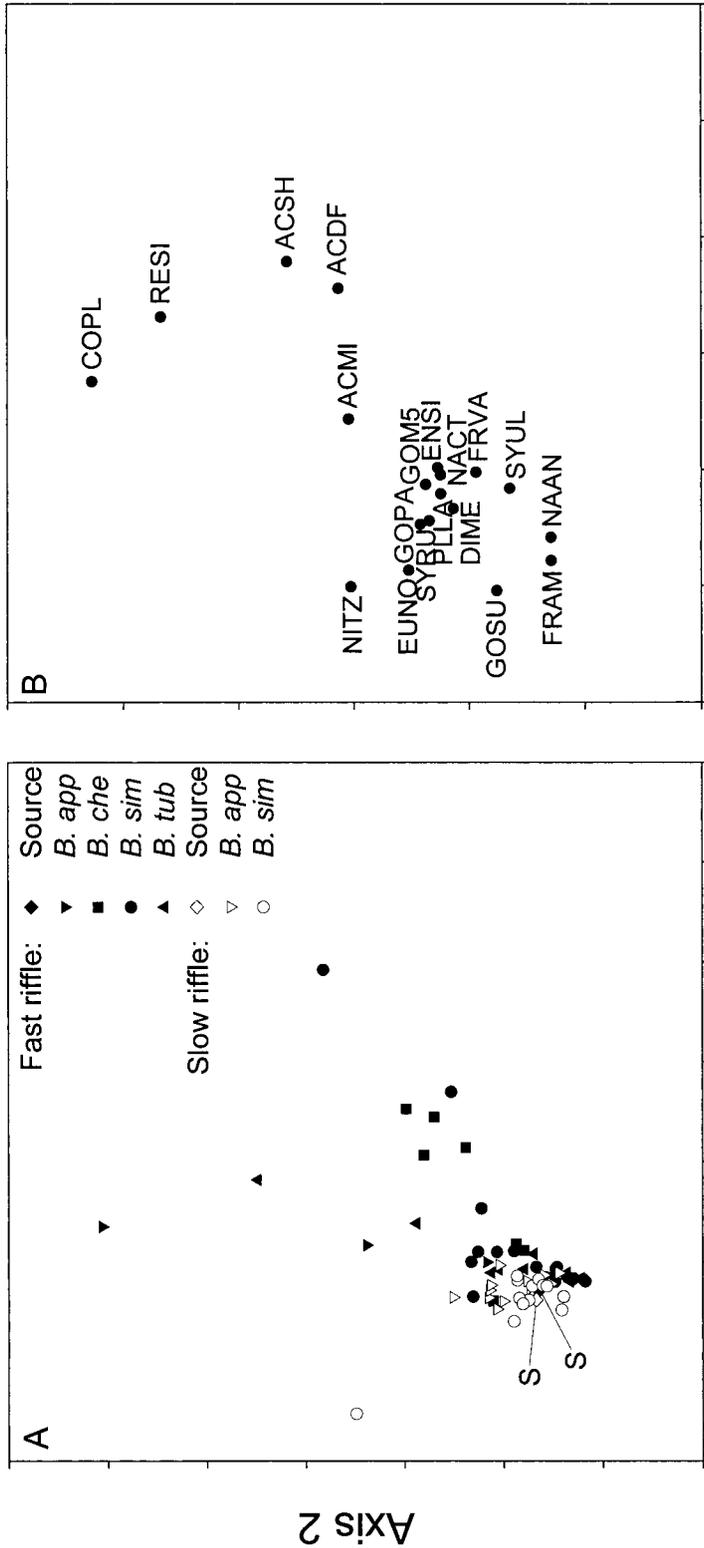
FIG. 3. Mean diatom biovolume (μm^3) ingestion (± 1 SE) per larval group at Brasstown Falls (A), Cataloochee Creek (B), and Chattooga River (C). Within a panel, columns with similar lower-case letters do not differ significantly ($p \geq 0.05$). Abbreviations as in Table 1.

FIG. 4.   A.—Two-dimensional nonmetric multidimensional scaling plot of Bray–Curtis distances among larval gut and source (S) diatom samples at Cataloochee Creek, North Carolina. Stress = 0.071. B.—Ordination of common diatom species from *Blepharicera* diets and source diatom samples at Cattaloochee Creek. Abbreviations of *Blepharicera* as in Table 1, of diatoms as in Table 3.

Table 5. Intra- and interhabitat pairwise diet comparisons (*p*-values) among larval groups of *Blepharicera* at Cataloochee Creek, North Carolina, using Mantel permutation procedures. Abbreviations as in Table 1. * = significant after sequential-Bonferroni correction for multiple comparisons (α = 0.05).

		Fast riffle				Slow riffle	
		B. app	*B. che*	*B. sim*	*B. tub*	*B. app*	*B. sim*
Fast riffle	*B. app*	–	0.055	0.052	0.078	0.013	0.027
	B. che	–	–	0.047	0.016	0.001*	0.002*
	B. sim	–	–	–	0.46	0.38	0.27
	B. tub	–	–	–	–	0.01	0.026
Slow riffle	*B. app*	–	–	–	–	–	0.066

the slow riffle, though the magnitude of the difference was small (Fig. 3B).

Chattooga River

Ordination.—NMDS generated a 2-dimensional ordination with stress value <0.1 (Fig. 5). Larval gut samples from the 2 microhabitats were distinguished primarily along axis 2 in ordination space (Fig. 5A). In the bedrock chute, the small, chain-forming diatom *F. vaucheriae* and the chain- and rosette-forming diatoms *S. rumpens* and *S.* cf. *ulna* dominated diets of *B. corniculata* and *B. similans* (Fig. 5A,B). *Blepharicera* from the bedrock chute ingested disproportionately greater biovolumes of *S.* cf. *ulna*, *S. rumpens*, and the small, adnate diatom *A. minutissimum*, compared to availability of those species on the substratum (Fig. 5A,B). In the slow riffle, *B. separata* dietary assemblages were dominated by *A. minutissimum* (Fig. 5A,B); in contrast, the diatom source sample was dominated by the larger diatoms *S.* cf. *ulna* and *S. rumpens* (Fig. 5A,B).

MPP.—The 2 microhabitats at Chattooga River were significantly different, based on collective larval dietary assemblages (MPP, *p* = 0.0001). Significant pairwise differences between *B. separata* (slow riffle) and each species from the bedrock chute (Table 6) were partly caused by the greater proportion of *A. minutissimum* in *B. separata* diets. In addition, a significant dietary difference was detected between *B. corniculata* and *B. similans* that co-occurred in the bedrock chute (Table 6). This difference was partly caused by the greater importance of *A. minutissimum* in the diet of *B. similans*.

Total diatom ingestion.—*Blepharicera separata* ingested the greatest diatom biovolume per individual, despite the fact that their diet consisted primarily of the small diatom *A. minutissimum*

(Fig. 3C; Table 3). *Blepharicera separata* ingested more diatom frustules than any other larval group across the 3 sites (AJA, unpublished data). No difference in total diatom ingestion was detected between *B. corniculata* and *B. similans* that co-occurred in the bedrock chute (Fig. 3C).

## Discussion

Dietary patterns of sympatric Blepharicera

Larval *Blepharicera* species in the southern Appalachian Mountains exhibited a striking degree of temporal and spatial overlap. In contrast to our hypothesis that dietary differences would be most disparate between larval congeners that co-occurred in a microhabitat, within-microhabitat dietary differences between *Blepharicera* species were evident in only 1 of 6 microhabitats (Chattooga River, bedrock chute) where multiple species occurred. Data from 5 of 6 microhabitats inhabited by multiple species suggested that *Blepharicera* species do not partition food resources to facilitate coexistence within microhabitats.

There was substantial evidence for microhabitat effects on *Blepharicera* dietary assemblages. Significant between-microhabitat differences in larval dietary assemblages were detected at 2 of 3 sites (Brasstown Falls and Chattooga River). Microhabitat was an especially important determinant of *Blepharicera* dietary assemblage at Brasstown Falls. *Blepharicera similans* was abundant in 3 microhabitats at Brasstown Falls, and each of the 3 *B. similans* groups had a distinct dietary assemblage. Likewise, dietary assemblage was distinct between *B. diminutiva* groups from the crash zone and hygropetric zone. At Chattooga River, between-microhabitat compar-
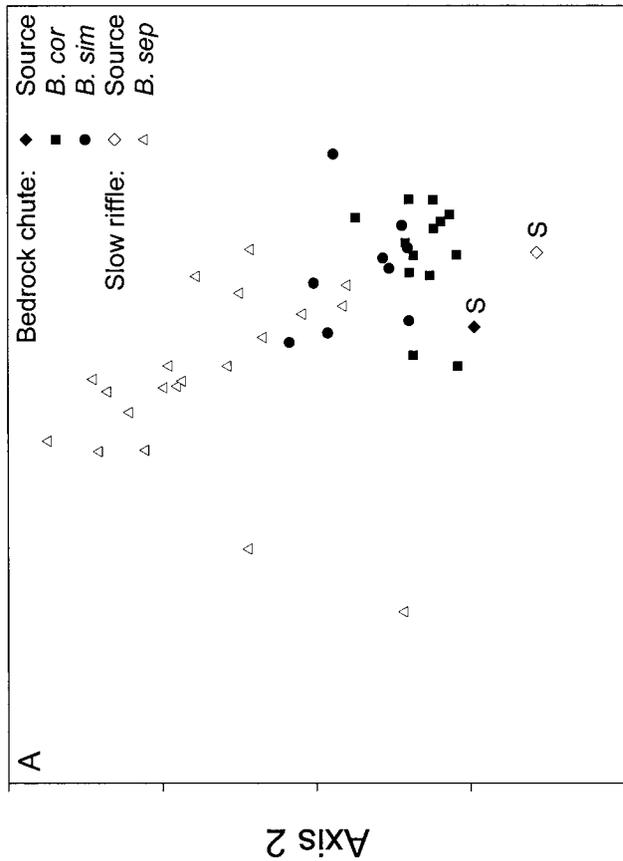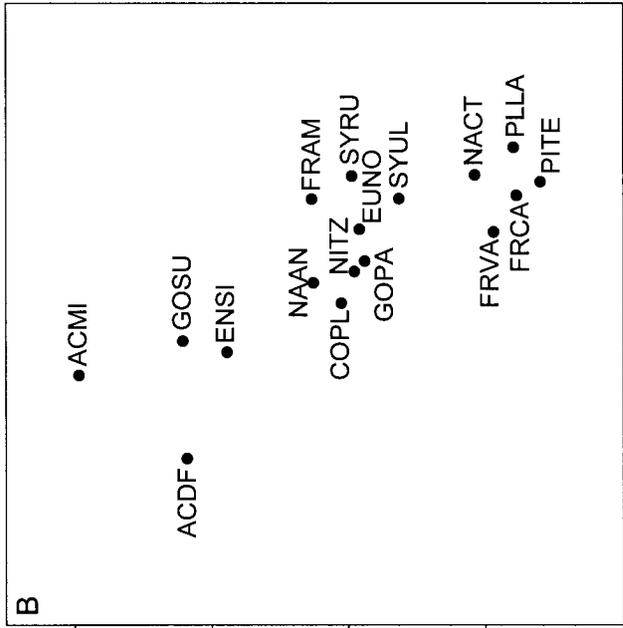
FIG. 5. A.—Two-dimensional nonmetric multidimensional scaling plot of Bray–Curtis distances among larval gut and source (S) diatom samples at Chattooga River, South Carolina. Stress = 0.084. B.—Ordination of common diatom species from *Blephaicera* diets and source diatom samples at Chattooga River. Abbreviations of *Blephaicera* as in Table 1, of diatoms as in Table 3.

TABLE 6. Intra- and interhabitat pairwise diet comparisons (*p*-values) among larval groups of *Blepharicera* at Chattooga River, South Carolina, using Mantel permutation procedures. Abbreviations as in Table 1. * = significant after sequential-Bonferroni correction for multiple comparisons (α = 0.05).

		Bedrock chute		Slow riffle
		B. cor	*B. sim*	*B. sep*
Bedrock chute	*B. cor*	–	0.016*	0.0001*
	B. sim	–	–	0.0002*

isons were confounded by species effect on diet because no *Blepharicera* species occurred in both microhabitats. Among our sites, microhabitat and substratum characteristics were most comparable among fast and slow riffles at Cataloochee Creek, where no intermicrohabitat differences in *Blepharicera* dietary assemblage were detected. The collective data emphasized the importance of substratum and microhabitat characteristics in determining *Blepharicera* dietary assemblage.

Within-microhabitat differences in total biovolume ingestion were detected between *Blepharicera* species in 3 of 6 microhabitats that supported multiple species. In general, differences were not consistent across microhabitats, which made them difficult to interpret. For example, in the crash zone at Brasstown Falls, *B. similans* ingested considerably greater biovolume than *B. diminutiva*; however, no difference was detected between the 2 species in the hygropetric zone. Likewise at Cataloochee Creek, *B. appalachiae* ingested greater biovolume than *B. similans* in the slow riffle, but no difference was detected between the 2 species in the fast riffle. No within-microhabitat differences in dietary assemblages were detected between larval groups, so interspecific differences in total biovolume ingestion reflected greater overall diatom ingestion by 1 species rather than differential ingestion of large diatoms by that species. Information on larval feeding rates, gut clearance rates, and microscale distribution of larvae and diatoms on substrata would have complemented these data and possibly made them easier to interpret.

Further evidence for a microhabitat effect on *Blepharicera* diets was manifested through patterns of total diatom biovolume ingestion at Brasstown Falls and Cataloochee Creek. At Brasstown Falls, decreasing total biovolume in diets of *B. similans* from the crash zone, hygropetric zone, and cascade, respectively, suggested a strong microhabitat effect on total biovolume ingestion. Likewise at Cataloochee Creek, *B. appalachiae* and *B. similans* from the fast riffle ingested significantly greater diatom biovolumes than their conspecifics from the slow riffle. Intermicrohabitat differences in total diatom ingestion probably reflect differences in source diatom cell density, which we did not measure.

There were substantial differences between diatom assemblages of *Blepharicera* diets and the forage base for several larval groups, based on ordination scores. Differences were most pronounced at Brasstown Falls and the Chattooga River. Deviations were often attributed to disproportionately greater biovolumes of small, adnate and prostrate diatom species (e.g., *Achnanthes* sp. #5, *Achnanthes deflexa* v. *alpestris*, *Achnanthidium minutissimum*, or *Cocconeis placentula* v. *lineata*) in larval diets compared to availability of those species on the substratum. Small size and growth form (adnate, prostrate, or short-stalked) typically preclude these diatom species from ingestion by invertebrate grazers (Dickman 1968, Nicotri 1977, Peterson 1987, Steinman et al. 1987). Inaccessibility of these diatoms to grazers also reflects the grazer's mouthpart morphology (Steinman 1996, Peterson et al. 1998). Peterson et al. (1998) suggested that "ingestion-resistant" diatom species (i.e., species with adnate or prostrate growth forms) can be digested more easily by grazers than "ingestion-susceptible" species (i.e., species with more conspicuous growth forms), in some cases. Dietary assemblage data, mouthpart structure, and evidence of mandibular attrition (Fig. 1) should establish *Blepharicera* larvae as true scrapers capable of ingesting otherwise ingestion-resistant diatom species.

Coexistence and competition among sympatric *Blepharicera*

Competition among grazers is presumed to be an important determinant of community structure and function in stream ecosystems (McAuliffe 1984, Hart 1985, Lamberti et al. 1987, Dudley et al. 1990). A critical assumption of competition theory that we made no effort to measure is that resources are available in limited supply (Birch 1957). Space and food could be

potential sources of competition among sympatric *Blepharicera* species because of their habitat restrictions. In western streams, *Blepharicera* compete for space with macroalgae (Dudley et al. 1986) and *Simulium* Latreille larvae (Dudley et al. 1990). Competition for space with *Simulium* decreased total diatom ingestion of *B. micheneri* by 60% (abundance), which ultimately decreased *B. micheneri* secondary production by ~50% (Dudley et al. 1990). Dudley et al. (1990) also reported significant inhibition of larval growth resulting from intraspecific competition among *B. micheneri* individuals. In western North American streams, where blepharicerid diversity is considerably less than in eastern North American streams, intra- and interspecific competition clearly affect blepharicerid populations. Thus, it seems possible that some of these same phenomena might influence structure of *Blepharicera* populations in eastern streams, where diversity is considerably greater.

It also remains possible that overlap in resource use (time, space, and food) among *Blepharicera* narrows the ecological breadth of 1, several, or all sympatric species. For example, *Blepharicera* diversity is considerably less in the central Appalachians than it is in the southern Appalachians. In central Appalachia, *B. appalachiae* occupies a broad range of microhabitats, including high-current-velocity riffles (Courtney 2000). In the southern Appalachians, where *Blepharicera* diversity is greater, *B. appalachiae* seems to be restricted to rocks in slow currents—the few *B. appalachiae* larvae that occupy faster currents are often restricted to less-exposed surfaces and undersides of rocks (Courtney 2000). If these observations are accurate and can be validated experimentally, then competition for space is the likely mechanism for the observed habitat displacement of *B. appalachiae* from central to southern Appalachia (Connell 1980). We measured resource overlap directly, which by itself is not sufficiently sensitive for detecting competition because species can overlap in their use of several resources and not be in competition (Menge 1979). The coexistence of sympatric *Blepharicera* in southern Appalachian streams could persist through sufficient divergence in some other relevant, though unmeasured, dimension of the multidimensional niche space (Pianka 1975, Connell 1980).

Microhabitat characteristics of Blepharicera

We identified microhabitats primarily by quantitative and qualitative variation in flow characteristics. At Cataloochee Creek and Chattooga River, mainstream current velocity distinguished fast and slow microhabitats, whereas qualitative differences in substratum exposure differentiated microhabitats at Brasstown Falls. Distribution of *Blepharicera* within a stream seems to be affected directly by characteristics of flow, including current velocity; however, the extent to which *Blepharicera* distribution reflects history, competitive interactions, or resource distribution remains unknown. Stevenson (1996) suggested that current velocity can indirectly shape invertebrate distribution via direct effects on algal species composition and density. Poff and Ward (1992), however, found that although algal distribution was a clear determinant of fine-scale *Agapetus* distribution, current velocity only affected source algal assemblages when grazers were absent. The effects of current on benthic algae are considered to be positive up to ~50 cm/s (Stevenson 1996), ~½ the velocity of slow microhabitats frequented by *Blepharicera* in our investigation. Fast and slow are obviously relative terms and, unfortunately, fast and slow qualifications described in current literature are considerably slower than those measured in our study (Stevenson 1996 and references therein). Investigations into effects of extreme current on density and distribution of rheophilous algae and invertebrate grazers (e.g., *Blepharicera*) are a prerequisite to understanding the complex relationships between the 2 groups (Poff and Ward 1995, Hart and Finelli 1999). In addition to accounting for algal cell densities on substrata, reciprocally transplanting marked conspecifics between microhabitats might afford insight into the effect of current velocity on *Blepharicera* grazing patterns. Also, modification of our sampling technique to include more precise characterization of local hydraulic environments (Wetmore et al. 1990) and estimation of microscale variation in current velocity around individual rocks relative to larval and algal distribution might have increased the resolution of our data.

Most of the evidence from our study suggests that sympatric *Blepharicera* species overlap broadly in time, space, and diatom ingestion. The competitive exclusion principle insists that

sympatric *Blepharicera* species cannot occupy the same ecological niche unless resources are unlimited in supply. Rather than revealing how sympatric *Blepharicera* species coexist in southern Appalachian streams, our data seem to make the original research problem even more provocative. We showed compelling evidence that microhabitat and substratum characteristics can be important determinants of *Blepharicera* dietary assemblage. Additional observational and experimental data are necessary to reveal 1) the extent to which sympatric species overlap in their use of resources not measured in this study, 2) whether sympatric *Blepharicera* species in southern Appalachian streams are in competition and, if so, for which resources, and 3) whether population sizes of sympatric *Blepharicera* species are sufficient to limit resource availability in southern Appalachian streams.

Acknowledgements

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