Feeding ecology of larval net-winged midges (Diptera: Blephariceridae: *Blepharicera* Macquart)

from the southern Appalachian Mountains

by

Andrew James Alverson

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Iowa State University

This is to certify that the Master's thesis of

Andrew James Alverson

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

For my parents, W. Edward and Rebecca E. Alverson,
and my partner and wife, Lisa A. Alverson.

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ABSTRACT

Despite the widespread perception that the Blephariceridae (Diptera) are a rare and functionally homogenous family, a decade of collecting and surveying the southern Appalachian Mountains has revealed that the region has a diverse fauna consisting of 13 *Blepharicera* species; an unusually high degree of regional and local sympatry among congeneric species; and predictable patterns of spatial and phenological mechanisms of ecological isolation among congeners. I describe the feeding characteristics of 7 *Blepharicera* species distributed among 3 sites in southern Appalachia. The algal assemblage of larval diets was assessed to explore potential ecological isolation of congeners overlapping in space and time through partitioning of food resources and patterns of grazing efficiency among *Blepharicera* species. Data showed that larval blepharicerids are true scrapers that feed almost exclusively on diatoms, dietary differences among groups occupying different microhabitats, and differences in grazing efficiency among species.

Eight *Blepharicera* species inhabit Cataloochee Creek, North Carolina. Based on season of larval activity, species can be broadly distinguished as winter, spring, or summer types. I examined fourth-instar diets of 2 temporally isolated species that have relatively long larval activity periods and a protracted fourth-instar stadium. Dietary assemblage structure, larval grazing efficiency, and total diatom consumption were measured for *B. magna* (winter type) and *B. similans* (summer type) to investigate whether larval grazing patterns changed over time. Data showed that algal assemblages in diet of *B. magna* did not vary over time. Algal assemblages in the diet of *B. similans* varied significantly throughout its fourth-instar stadium. Furthermore, total diatom consumption by both species was greatest at midstage, and both species showed consistently low larval grazing efficiency, due to positive differential ingestion of adnate and prostrate diatom species. I also present general information about blepharicerid biology, emphasizing their importance in the structure and function of lotic ecosystems.

CHAPTER 1. GENERAL INTRODUCTION

Net-winged midges (Diptera: Blephariceridae) are a fascinating group of aquatic flies. Immatures occupy torrential streams, cascades, waterfalls, and hygropetric habitats. A fused head, thorax, and first abdominal segment (= cephalothorax) and the possession of six ventral suctorial discs render larvae among the most specialized torrenticolous insects. Pupae are also well-adapted for life in high current (rheophily), being dorsoventrally compressed, nearly perfectly streamlined [though see Pommen and Craig (1995)], and cemented immovably to substrata via a series of ventrolateral abdominal pads. Adults are relatively short-lived and are typically found on the undersides of leaves in the riparian vegetation near their natal stream. Adults resemble other nematocerous dipterans (e.g., Culicidae and Tipulidae), having exceptionally long legs and slender bodies.

In North America, there are 34 species of blepharicerids in 4 genera: *Agathon* von Röder (8 species), *Bibiocephala* Osten Sacken (1 species), and *Philorus* Kellogg (4 species) are western genera, whereas *Blepharicera* Macquart (21 species) is widespread (Hogue 1987, Courtney 2000). The Appalachian Mountains are home to the highest diversity of blepharicerids in North America. Sixteen species inhabit the region, 13 of which occur in the southern Appalachians (Courtney 2000). Poor taxonomic resolution has impeded meaningful ecological investigations of eastern *Blepharicera* in the past. Fortunately, descriptions of several new species and keys to all Appalachian species are available (Courtney 2000), permitting the taxonomic resolution necessary to study blepharicerid ecology.

Larval Blephariceridae graze on periphytic films that blanket submerged substrata. Robust mandibles and highly specialized maxillary structures allow larvae to scrape algae from the entire periphyton layer, including the periphytic understory (Courtney 1990, 1991). Little is known about the dietary characteristics of larval blepharicerids. Some studies suggest that diatoms comprise the major biotic component of larval diets (Tonnoir 1930, Alexander 1963, Brodsky 1980). Georgian and Wallace (1983) noted that "amorphous clumps" removed from

larval guts were actually solid masses of small diatom frustules. Dudley et al. (1990) considered diatom ingestion by *B. micheneri* Alexander as part of an investigation into interspecific competition with larval black flies (Simuliidae). Diatoms are a food source of exceptional quality, due in part to high lipid content and ease of digestibility and assimilation compared with bacteria and other algae (Kajak and Warda 1968, Hargrave 1970, Anderson and Cummins 1979, Fuller and Desmond 1997). Raw gut material from Appalachian blephariceriids shows that larval diets consist primarily of diatoms (A. J. Alverson, unpublished data).

Feeding ecology of sympatric Blepharicera

Despite relatively narrow habitat requirements and a presumably broad dietary overlap, local sympatry of 3 or more congeneric species is common at several sites in the southern Appalachian Mountains. The marked sympatry of Appalachian Blephariceridae is curious and deserving of formal investigation into potential mechanisms of ecological isolation among congeneric species. In this study, I provide a detailed description of the larval diets of several eastern *Blepharicera* species from 3 sites in southern Appalachia including Brasstown Falls, South Carolina; Cataloochee Creek, North Carolina; and Chattooga River, South Carolina. Diets of congeneric species within and between discrete microhabitats are contrasted. In addition, diatom assemblages of larval guts are compared with that of the forage base.

Temporal grazing patterns of larval Blepharicera

Eight *Blepharicera* species inhabit Cataloochee Creek, North Carolina. On the basis of larval activity period, the fauna can be separated into winter (*sensu* Kitakami (1950) and summer guilds. I chose the species with the longest larval activity period in each and documented their diets over several months. *Blepharicera magna* is a univoltine winter species. Larvae typically are active from early September through March (Courtney 2000). The first 3 larval stadia are short, and *B. magna* larvae overwinter as mature, fourth instars. In contrast, *B. similans* is a summer species, and some data suggest that *B. similans* is multivoltine at

several sites (Courtney 2000). Collection records demonstrate that the *B. similans* population at Cataloochee Creek is univoltine and that the larval period can span from May until September. In this study, we document the larval diets of *B. magna* and *B. similans* throughout their fourth-instar stadia. Larval dietary assemblages are compared with that of the forage base. In addition, total diatom consumption estimated and compared among larval groups.

Thesis organization

The thesis consists of 4 chapters, 2 of which will be submitted for publication. Chapter 1 provides a general overview, thesis organization, and references cited in the general introduction. Chapter 2 describes grazing patterns of sympatric *Blepharicera* larvae. Chapter 3 presents a description of temporal changes in the diets of *B. magna* and *B. similans*. Chapter 4 contains general conclusions and a research prospectus. To date, this study represents the most rigorous treatment available of any aspect of blepharicerid ecology. The primary author was responsible for the design and performance of the studies included in this thesis. All results and conclusions from these studies were interpreted and written into manuscript form by A. J. A. As per Article 8.2 of the International Code of Zoological Nomenclature (1999), this document is not issued for the permanent scientific record or for purposes of zoological nomenclature. Consequently, any species names contained herein should not be considered as published (*sensu* ICZN).

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CHAPTER 2. MICROHABITAT AND FEEDING CHARACTERISTICS OF LARVAL NET-WINGED MIDGES (DIPTERA: BLEPHARICERIDAE: *BLEPHARICERA*) FROM THE SOUTHERN APPALACHIAN MOUNTAINS

Andrew J. Alverson[1], Gregory W. Courtney[1], and Mark R. Luttenton[2]

Abstract. Despite the widespread perception that the Blephariceridae (Diptera) are a rare and functionally homogenous family, a decade of collecting and surveying the southern Appalachian Mountains has revealed that the region bears a diverse fauna, consisting of 13 *Blepharicera* species; an unusually high degree of regional and local sympatry among congeneric species; and predictable patterns of spatial and phenological mechanisms of ecological isolation among congeners. We describe the feeding characteristics of 7 *Blepharicera* species distributed among 3 sites in southern Appalachia. The algal assemblage of larval diets was assessed to explore potential ecological isolation of congeners overlapping in space and time through partitioning of food resources and patterns of grazing efficiency among *Blepharicera* species. Data showed that larval blepharicerids are true scrapers that feed almost exclusively on diatoms, dietary differences among groups occupying different microhabitats, and differences in grazing efficiency among species. We also present general information about blephariceHd biology, emphasizing their importance in the structure and function of lotic ecosystems.

Introduction

Net-winged midges (Diptera: Blephariceridae) are a widespread but small family, currently comprised of 27 genera and ~300 species (Zwick and Zwick 1998, Courtney 2000). In North America, there are 34 species of blepharicerids in 4 genera: *Agathon* von Röder (8

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[1]Iowa State University, Department of Entomology, Ames, Iowa 50011

[2]Grand Valley State University, Department of Biology, Allendale, Michigan 49401

species), *Bibiocephala* Osten Sacken (1 species), and *Philorus* Kellogg (4 species) are western genera, whereas *Blepharicera* Macquart (21 species) is widespread (Hogue 1987, Courtney 2000). Blepharicerids have garnered considerable interest among entomologists and aquatic biologists, which apparently reflects the group's unusual ecological and morphological characteristics. Despite the attention, a paucity of literature exists directly addressing blepharicerid ecology, hence the ensuing underappreciation of their importance in the structure and function of lotic ecosystems. Densities of immatures can exceed $1000/m^2$, making them a dominant grazer and often the most locally abundant insect (Johns 1996). Anderson's (1992) study of streams in Oregon's Cascade Range demonstrated that blepharicerids may be one of the most abundant insects in annual biomass production and, thereby, of substantive trophic importance. Furthermore, Courtney and Duffield (2000) demonstrated that blepharicerids are a trophic resource for lotic fish, reporting their high numerical abundance in the stomachs of trout from eastern and western North American streams. Finally, in a study of >500 North Carolina invertebrate taxa, Lenat (1993) calculated a general tolerance value of 0.2 (scale = 0–10) for "*Blepharicera* spp.," predicting the importance of individuals in this genus as sensitive bioindicators of stream quality.

Blepharicerid natural history

Blephariceridae represent perhaps the most specialized and well-adapted family of torrenticolous insects. Immature stages occupy the seemingly uninhabitable—thriving in cascades, at the bases of crashing waterfalls, and in currents that can exceed 400 cm/s (Craig 1966). The 4 larval instars are distinctive, characterized primarily by morphological adaptations to rheophilic life. A fused head, thorax, and first abdominal segment (=cephalothorax) keep the anterior larval body compact and within a more viscous region of the boundary layer. Six ventral suctorial discs ensure attachment to submerged substrata, usually cobble or bedrock. Blepharicerids require smooth surfaces to maintain sucker function (e.g., they adhere easily to glass), precluding them from sedimentary rock or surfaces otherwise

roughened with lichens, macroalgae, moss, or marl (Zwick 1977, Dudley et al. 1986). Macroalgae (e.g., *Cladophora* and *Nostoc*) have been shown to outcompete larval *Blepharicera* for space by effectively shading out potential food sources and rendering the substratum unsuitable for sucker attachment (Dudley et al. 1986). Pupae are also well adapted for life in currents, being dorsoventrally compressed and attached immovably to substrata via a series of ventrolateral abdominal pads. Adults resemble mosquitoes (Culicidae) or crane flies (Tipulidae), having exceptionally long legs and slender bodies. Their wings are characterized by a network of fine intercalary folds that inspired their common name, the net-winged midges. Adults are typically associated with riparian vegetation near their natal stream where they exhibit a variety of feeding habits—predation and nectarivory are common to some species, whereas others are nonfeeding.

Blephariceid larvae use highly specialized mouthparts (Fig. 2.1A) to graze on periphytic films that blanket submerged substrata. Based on meticulous observations of larvae in laboratory aquaria, Tonnoir (1930) was the first to document the blephariceid feeding mechanism, describing these larvae as "grazing like cattle in a paddock." Foraging behavior is characteristic and apparently predictable, consisting of a slow (~2 mm min^{-1}), forward, downstream progression as the cephalic division moves in a lateral, pendulumlike motion (Dudley et al. 1990, Frutiger 1998). Robust mandibles simultaneously move back and forth, scraping the substratum to dislodge epilithic algae (Tonnoir 1930, Arens 1989, Courtney 1990). Dissected mandibles from a recently ecdysed larva (Fig. 2.1B) and a mature larva (Fig. 2.1C) demonstrate the abrasive effect of this behavior on larval mouthparts. As the mandibles are extended forward, the maxillae (Fig. 2.1A, mxl) are simultaneously pressed against the substratum. When the mandibles are retracted, maxillae are drawn medially, sweeping dislodged food particles into the cibarium (Tonnoir 1930, Courtney 1990). A large, padlike labium (Fig. 2.1A, lbm) is thought to prevent posterior food escape (Courtney 1990).

Based on the widespread perception that blepharicerids are a functionally homogenous group restricted to riffles and glides in swift streams, one might expect broadly allopatric distribution patterns of species or populations. Despite relatively narrow habitat requirements and a presumably broad dietary overlap, local sympatry of 3 or more congeneric species is commonly observed at several sites throughout the southern Appalachian Mountains. One of these sites, Chattooga River, is home to 11 *Blepharicera* species. At least 3 species are present year-round, and in mid-spring as many as 6 species can be present (Table 2.1). The potential overlap in exploitation of finite resources is exacerbated by the structural homogeneity of immature *Blepharicera*, which presumably reflects the common need for certain structural adaptations given their unusual ecological restrictions (Courtney 2000). This structural homogeneity is particularly evident in the extremely conservative mouthpart structure observed across most genera of Blephariceridae. The marked sympatry of Appalachian Blephariceridae is curious and deserving of formal investigation into potential mechanisms of ecological isolation among congeneric species.

Ecological and reproductive isolation are common phenomena among sympatric stream invertebrates. Isolation of potential competitors has been revealed through differences in life history patterns (Cummins 1964, Anderson and Bourne 1974, Sweeney and Vannote 1981, Georgian and Wallace 1983, Courtney 1991, Wallace and Anderson 1996), longitudinal distribution (Hildrew and Edington 1979), microdistribution (Cummins 1964, 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 exploitation of food resources (Cummins 1964, Thut 1969, Williams and Hynes 1973, Hildrew and Edington 1979, Cummins and Merritt 1996) among several groups of aquatic invertebrates. Although similar isolation mechanisms have been reported for sympatric blepharicerids from various parts of the world, most investigations have focused on temporal and spatial segregation.

Temporal isolation of sympatric species has been observed in the Japanese (Kitakami 1950), Australian (Zwick 1977), and North American (Courtney 1991, 2000, Johns 1996) faunas. Based on larval activity period, Kitakami (1950) distinguished Japanese species as winter, summer, or perennial types. All subsequent life cycle classifications have been variants of the Kitakami (1950) scheme, including those of Johns (1996) and Courtney (2000) for the Appalachian fauna. Appalachian species can generally be classified as winter, spring, or summer types (Johns 1996, Courtney 2000). A qualitative summary of the life-cycle characteristics of *Blepharicera* species occurring at our study sites is provided in Table 2.1.

Spatial isolation (at a particular point in time) of sympatric Blephariceridae is also well documented. Based on observations of Japanese fauna, Kitakami (1950) was perhaps the first to establish a habitat classification scheme for immature blepharicerids. Each species was classified according to 1 of 3 habitat preferences: common submersed type, found in association with completely submerged substrata; hygropetric type, found on exposed rock surfaces in splash zones along—but distinctly separate from—stream banks and waterfalls; and cascade type found in rushing or spraying water such as in or adjacent to waterfalls and cascades (Kitakami 1950). There is a gradient between Kitakami's (1950) hygropetric and cascade types, often making the two difficult to distinguish. Kitakami's (1950) classification scheme was adopted in part by Zwick (1977) who observed species-specific microhabitat preferences and longitudinal separation among the Australian blepharicerid fauna; similar patterns were later observed in the Italian and Corsican faunas (Zwick 1980). Appalachian fauna exhibit consistent patterns of species-specific microhabitat preferences as well (Courtney 2000). Generalized microhabitat characteristics for species that inhabit our study sites are summarized in Table 2.1. Kitakami (1950) and Zwick (1977, 1980) also have suggested temperature as a determinant of longitudinal distribution of immatures.

Brodskiy and Omorov (1972) noted distinct longitudinal separation of sympatric net-winged midges and mountain midges (Deuterophlebiidae) along the Ak-Bura and Kichik-Alay

rivers in central Asia. Differences in altitude, water temperature, flow rate, substratum, and riparian vegetation were thought to account for the distribution patterns (Brodskiy and Omorov 1972). Courtney (1991) also noticed a high degree of sympatry and corresponding spatial separation among mountain midges and net-winged midges in western North American streams. Although his hypothesis has yet to be tested, Courtney (1990, 1991) suggested that subtle differences in mouthpart morphology between taxa result in differences in resource use, effectively reducing potential competition for food. Larval mountain midges (Deuterophlebiidae) apparently move over substrata relatively quickly, browsing (*sensu* Lamberti et al. 1987a) on filamentous algae and elements of the periphyton canopy whereas larval Blephariceridae are scrapers (*sensu* Lamberti et al. 1987a), restricting their feeding to a smaller area and extracting from the entire periphyton layer, including the periphytic understory (Courtney 1990, 1991).

No studies have explored dietary differences in facilitating the coexistence of sympatric blepharicerids; in fact, little is known about the dietary characteristics of larval blepharicerids. Some studies suggest that diatoms comprise the major biotic component of larval diets (Tonnoir 1930, Alexander 1963, Brodsky 1980). Georgian and Wallace (1983) noted that "amorphous clumps" removed from larval guts were actually solid masses of small diatom frustules. Dudley *et al.* (1990) considered diatom ingestion by *B. micheneri* Alexander as part of an investigation into interspecific competition with larval black flies (Simuliidae). Diatoms are a food source of exceptional quality, due in part to high lipid content and ease of digestibility and assimilation compared with bacteria and other algae (Kajak and Warda 1968, Hargrave 1970, Anderson and Cummins 1979, Fuller and Desmond 1997). Raw gut material from Appalachian blepharicerids shows that larval diets consist primarily of diatoms and some unidentifiable detritus (A. J. Alverson, unpublished data).

Georgian and Wallace (1983) identified a guild of 5 grazing insects in a southern Appalachian stream and clearly demonstrated temporal isolation of *B. williamsae* and

Blepharicera spp. *Blepharicera* spp. was thought to comprise at least 2 species, drawing attention to the poor taxonomic resolution of the group. In fact, the Appalachian Mountains are home to the highest diversity of blepharicerids in North America. Sixteen species inhabit the region, 13 of which occur in the southern Appalachians (Courtney 2000). The result is a striking degree of regional and local sympatry that begs the question of how animals with such restricted ecological requirements are able to coexist. Fortunately, descriptions of several new species and keys to all Appalachian species are available (Courtney 2000), permitting the taxonomic resolution necessary to investigate possible mechanisms of ecological isolation among sympatric species. Based on Courtney (2000), Georgian and Wallace's (1983) *Blepharicera* spp. was a composite of potentially 5 species and Lenat's (1993) *Blepharicera* spp. could have included as many as 12 species. In this study, we attempt to provide a clearer understanding of larval blepharicerid ecology by documenting the larval diets of several eastern *Blepharicera* species; comparing and contrasting the diets of congeneric species within and between discrete microhabitats; and comparing and contrasting the diatom assemblages of larval guts with that of the forage base.

Methods

Study sites

We chose 3 sites in the southern Appalachian Mountains based on habitat characteristics and knowledge of blepharicerid faunal diversity and phenology. Diversity, phenology, and habitat data of blepharicerid fauna at each site are summarized in Table 2.1. Brasstown Creek (34°42′N, 83°18′W), a third-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 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 the riparian vegetation and overhanging the

cascades and waterfalls; in addition, various pine (*Pinus* spp.) and hardwood species are scattered throughout the riparian zone. The second site, Cataloochee Creek (35°40′N, 83°04′W), is a fourth-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]. The third site, Chattooga River (34°48′N, 83°18′W), is a fifth-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 the Chattahoochee and Sumter National Forests, respectively. The Chattooga supports the highest known blephariceri diversity of any stream sampled to date. Chattooga River is the 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, various ferns [hayscented fern, *Dennstaedtia punctilobula* (Michaux) Moore; cinnamon fern, *Osmunda cinnamomea* L.; Christmas fern, *Polystichum acrostichoides* (Michaux) Schott; and New York fern, *Thelypteris noveboracensis* L.], and several species of sedges.

Field collection

All samples were collected in mid-May 1998, when the greatest degree of overlap in larval activity should occur. Each site was sampled midday [1300–1700 hours (EST)] to eliminate the potential complication of fluctuating diurnal feeding rates. Because blephariceri distribution within streams is often patchy and nonrandom, sampling was based primarily on the presence of larvae and was, therefore, nonrandom. Our samples, in essence, are representative of ideal blephariceri habitat. Within a microhabitat, rocks were randomly

selected and blepharicerids were removed individually with forceps and preserved in 6:3:1 (95% ethanol:water [collection]:10% formalin) solution. Because of difficulties in field identification of larvae, all larvae beyond the second instar were collected (due to their small size, collection of early instars is possible only by thoroughly washing rocks). This also prevented sampling bias toward large individuals. After removal of larvae, ambient algae were removed with a toothbrush and preserved in 6:3:1 solution. Algae were collected from areas that varied with larval distribution on substrata. Although this collection method impeded cell density estimates, it was intended to minimize the impact that potentially aberrant diatom "patches" falling outside of the immediate larval grazing pasture had on estimation of ambient community structure. All larval and algal collections consisted of pooled material from 2 or 3 rocks or a single exposure of bedrock (e.g., Brasstown Falls, Chattooga River "chute"). For the latter, rushing water was shunted away, enabling collection of larvae and algae, with a modified polyvinylchloride (PVC) pipe fitted with a soft, pliable collar. Throughout this article, individual larvae and ambient (source) collections are referred to as samples, and the sum of larval conspecifics from a microhabitat are referred to as groups. The number of individuals per group (n) is noted parenthetically following the insect's Latin name in "Collection" in Results section. When possible, free-stream current velocity was measured directly above each rock sampled. These measurements were then averaged over a microhabitat, with the range not exceeding 20 cm/s.

Laboratory preparation and analyses

Fourth-instar larvae consume considerably more food than earlier instars (A. J. Alverson, unpublished data), a finding consistent with that of Georgian and Wallace (1983), who found maximum production of *B. williamsae* at the end of its larval period. This attribute seems to be shared by other insect groups (Waldbauer 1968). Furthermore, larvae discontinue feeding and empty their guts prior to larva–larva molts and larva–pupa molts (A. J. Alverson, unpublished data); therefore, we examined only midstage, fourth-instar larvae. Prior to

dissection, body length and head capsule width of each larva were recorded. The entire gut was then dissected out with the aid of 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 mounted on a slide by using the mounting medium Naphrax. Source material was acid-cleaned according to Patrick and Reimer (1966), air dried onto a coverslip, and slide-mounted by using Naphrax. All samples were examined at 600× with a Nikon E800 compound microscope. At least 1000 diatom valves per sample were randomly identified and enumerated using standard taxonomic references (Hustedt 1930, Patrick and Reimer 1966, 1975, Krammer and Lange-Bertalot 1991a,b, Krammer and Lange-Bertalot 1997a,b) and various floristic studies of the diatom species from the southeastern United States (Camburn and Lowe 1978, Kociolek 1982, Lowe and Kociolek 1984). Slides were then scanned to record rare taxa. If a gut sample consisted of <1000 diatom valves, the entire slide was counted. Valves rather than frustules were counted to account for potential differences in propensity of diatom taxa to separate from an intact frustule into valves. At least one-half of a valve had to be present to be included in the counts. Diatom images for major taxa are available in Alverson (2000).

Statistical analyses

Raw counts were translated into absolute biovolumes with biovolume estimates generated in BIOVOL (Kirschtel 1996). Critical measurements were taken for 20 cells each for common taxa and as many cells as possible for each rare taxon, and the average of these measurements was used for biovolume calculations. Data were then standardized by conversion of absolute biovolumes to proportions of the total (i.e., relative biovolumes). Diatom taxa with an average of ≥2% of the relative biovolume of at least 1 larval group or source sample were included in statistical analyses. Each site was analyzed independently.

Diet overlap.—Gut and source samples were ordinated with nonmetric multidimensional scaling (NMDS; Kruskal and Wish 1978) to evaluate visually whether the algal assemblage of

larval guts differed between groups and from that of the corresponding source sample. Nonmetric multidimensional scaling requires very few assumptions and is especially useful when one insists only on preserving a monotonic relationship between biological distance and plot distance. With a user-defined dissimilarity (distance) measure, NMDS first transforms a data matrix of n samples by p species into a triangular distance matrix of all possible pairwise sample comparisons. These pairwise sample distances are rank ordered from lowest to highest (or vice versa) and then ordinated on rank similarity alone (Kenkel and Orlóci 1986, Clarke 1993). The result is a graphical representation of samples, where the arrangement of sample points in low-dimensional plot approximates the biological distance among samples while preserving their rank order (Kenkel and Orlóci 1986, Clarke 1993). A measure of disagreement between the distance matrix and the ordination is given by the stress coefficient, for which values <0.1 are desirable (Clarke 1993). Ordinations presented in this article are based on pairwise sample distances calculated using the Bray–Curtis metric on untransformed data.

Multiresponse permutation procedures (MRPP; Mielke *et al.* 1981) with Bray–Curtis distance were used to test the null hypothesis of no difference in dietary assemblage among larval groups. Multiresponse permutation procedures also were used to evaluate whether microhabitats could be distinguished on the basis of larval samples; these interhabitat comparisons were achieved by grouping all larval samples from each habitat and then running MRPP on designated habitat groups. The following is a brief synopsis of MRPP condensed from Mielke *et al.* (1981) and McCune and Mefford (1999). First, a mean within-group distance is calculated for each individual group. A weighted mean within-group distance, delta (δ), is then calculated for the entire data set and compared against an approximated δ distribution to evaluate the probability of obtaining the observed δ by chance alone—this value is the reported p value. A measure of effect size is given by the chance corrected within-group agreement (A):

$$A = 1 - \frac{\delta_{observed}}{\delta_{expected}}$$

where $\delta_{expected}$ is the mean of the δ distribution. More tightly clustered groups have a smaller $\delta_{observed}$, and as a result, A increases toward 1 ($A = 1$ is the theoretical maximum, meaning all within-group objects are identical). Likewise, more diffuse groups have a larger $\delta_{observed}$ and smaller A value (when $A = 0$, the null hypothesis of no difference between groups is true). In the seemingly unlikely event that $\delta_{observed}$ is greater than expected by chance, then $A < 0$. For community data, A values are typically <0.1, and $A > 0.3$ is considered high (McCune and Mefford 1999). Nonmetric multidimensional scaling and MRPP were run with PC-ORD (version 4; MjM Software Design, Gleneden Beach, Oregon); the algorithms for both procedures are summarized in McCune and Mefford (1999).

Grazing efficiency.—Grazing efficiency (*sensu* Peterson *et al.* 1998) was assessed with the Bray–Curtis measure of similarity (Bray and Curtis 1957). Mean Bray–Curtis similarities were calculated for each larval group. The Bray–Curtis similarity ($S_{l,s}$) between the diatom assemblage of a larval gut (l) and its corresponding source sample (s) is given by

$$S_{l,s} = 1 - \frac{\sum_{j=1}^{p} |X_{l,j} - X_{s,j}|}{\sum_{j=1}^{p} (X_{l,j} + X_{s,j})}$$

where $X_{l,j}$ and $X_{s,j}$ equal the relative biovolume of diatom j in the larval gut and source sample, respectively, and p equals the number of diatom taxa being compared. The equation returns a proportion coefficient ranging from 0 (dissimilar) to 1 (similar) (Krebs 1989). The Bray–Curtis metric weighs abundant dietary attributes more heavily than rare ones, is insensitive to joint absences, and is generally regarded as a stable, well-behaved distance

measure (Field et al. 1982, Faith et al. 1987, Boyle et al. 1990). Interpoint distances between larval gut and source samples in ordination space provide a visual approximation of larval grazing efficiency. The total algal biovolume ingested per individual also was estimated and compared among larval groups. These estimates were made by consideration of total number of diatom valves enumerated, number of fields analyzed, field diameter, and total area. A 1-factor analysis of variance (ANOVA) was used to assess intra- and interhabitat differences in Bray–Curtis similarity coefficients and log-transformed total biovolume estimates among larval groups. Because estimates of the ambient community were based on 1 sample, they were excluded from all inferential statistical methods, including MRPP. 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 group comparisons were made with 2 sample t tests, with the least squares means (LSMEANS) statement in the GLM procedure. For MRPP and ANOVAs, the Bonferroni method was used to maintain an experimentwise type I error rate of $\alpha = 0.05$. Post Bonferroni-corrected type I error rate (α') is presented for each site, but because of the extremely conservative nature of the Bonferroni method and the arbitrariness of choosing the initial $\alpha = 0.05$, some potentially important effects that lack statistical significance are presented.

Results

Brasstown Falls

Collection.—Three distinct microhabitats were sampled at Brasstown Falls, yielding a total of 5 larval groups. The first microhabitat sampled (crash zone) was located at the base of Brasstown's lower falls. Emergent bedrock exposed to the persistent crash of falling water was inhabited by 2 species, *B. diminutiva* (n = 9) and *B. similans* (n = 11). The hygropetric fauna, which included *B. diminutiva* (n = 14) and *B. similans* (n = 9), was then sampled from an exposure of bedrock adjacent to the cascade. *Blepharicera similans* (n = 18) also was found

directly in the cascade, which was characterized by continuous, rapidly flowing water of ~5 cm depth.

Diet overlap.—The algal assemblage of larval diets varied significantly among the 3 microhabitats (MRPP; $A = 0.25$, $p < 0.0001$). Significant interhabitat differences in larval diets also were detected through pairwise comparisons of larval groups (Table 2.3). Larval gut samples from the crash zone were distinguished from both the hygropetric and cascade samples along axis 2 and axis 3 in the NMDS sample ordination (Fig. 2.2A). In the crash zone, *Epithemia adnata* accounted for displacement of larval gut and source samples along axis 2 and axis 3; disproportionately large biovolumes of the small, adnate diatom *Achnanthidium minutissimum* in larval diets contributed also to the displacement of crash zone samples along axis 3 (Fig. 2.2B). Larval gut samples from the hygropetric and cascade microhabitats were somewhat displaced along axis 1 and axis 3 (Fig. 2.2A). The larger contribution of *Gomphonema* sp. #1 to larval diets of hygropetric groups compared with the *B. similans* cascade group accounted for much of the displacement along axis 3 (Fig. 2.2B). Finally, larval gut samples of *B. diminutiva* and *B. similans* that co-occurred in the crash zone and hygropetric microhabitats overlapped broadly in ordination space (Fig. 2.2A) and did not differ significantly (Table 2.3).

Grazing efficiency.—Examination of larval grazing efficiency at Brasstown Falls revealed several important findings. First, the algal source sample from the cascade at Brasstown Falls consisted primarily of unidentified bryophytes and too few diatoms to estimate accurately the community structure. Thus, we were unable to measure grazing efficiency for the *B. similans* cascade group. Although bryophytes dominated the source collection, their abundance apparently was not so great as to exclude larval *Blepharicera*. In the other 2 microhabitats, the algal assemblage of larval guts showed an ~40% average Bray–Curtis similarity to that of the ambient algal community (Fig. 2.5). For crash zone groups, low grazing efficiency was attributable to the disproportionately low biovolumes of *Synedra* sp. cf. *ulna* and large

biovolumes of *A. minutissimum* in larval diets relative to their availability on the substratum (Fig. 2.2B). In the hygropetric zone, larvae fed on disproportionately large biovolumes of *Gomphonema* sp. #1 relative to its availability; in addition, 3 large diatom taxa (*Diatoma vulgaris*, *Navicula lanceolata*, and *Navicula tripunctata*) were numerically abundant in the source collection and absent from larval guts (Fig. 2.2B). In the 2 microhabitats where *B. diminutiva* and *B. similans* co-occurred, no significant differences in larval grazing efficiency were detected (Fig. 2.5). The large algal biovolumes ingested by the *B. similans* cascade group reflect the high abundance of the large diatom *E. adnata* in larval diets (Table 2.2, Fig. 2.5).

Cataloochee Creek

Collection.—Two distinct microhabitats were sampled at Cataloochee Creek. *Blepharicera appalachiae* (n = 4), *B. cherokea* (n = 7), *B. similans* (n = 20), and *B. tuberosa* (n = 11) were collected from a "fast" riffle where the free-stream current velocity was 232 cm/s. The free-stream current velocity at the second microhabitat was 90 cm/s, and *B. appalachiae* (n = 12) and *B. similans* (n = 13) were collected from this "slow" riffle.

Diet overlap.—Significant differences in the gut contents of larvae occupying different microhabitats were detected (MRPP; $A = 0.05$, $p < 0.0001$) and visualized in their subtle displacement along axis 1 in the sample ordination (Fig. 2.3A). Furthermore, all pairwise interhabitat comparisons of larval groups showed significant differences of varying probability and effect size (Table 2.4). Spatial overlap of larval congeners was most acute in Cataloochee Creek's fast riffle where 4 *Blepharicera* species were collected. Despite the overlap, no clear pattern of food partitioning was detected among larval congeners within this microhabitat (Table 2.4). Slight, marginally significant difference were detected in the diets of *B. appalachiae* and *B. similans* that co-occurred in the slow riffle (Table 2.4).

Grazing efficiency.—Evaluation of larval grazing efficiency at Cataloochee Creek revealed 3 important findings. First, the algal assemblage of larval gut and source samples showed high

Bray–Curtis similarities, and this pattern was relatively consistent among all larval groups (Fig. 2.5). The overlap of larval gut and source samples in the sample ordination also suggests a high larval grazing efficiency among larval groups (Fig. 2.3A). Second, though Bray–Curtis similarity coefficients did not vary appreciably across habitats, estimates of mean algal biovolume ingested per individual were higher for larvae from the fast riffle than for conspecifics collected from the slow riffle (Fig. 2.5). The large standard errors that accompany measures of grazing efficiency for the fast *B. appalachiae* group probably reflect small sample size ($n = 4$). Overall, neither the algal assemblage of larval gut samples nor larval grazing efficiency tended to vary appreciably among larval groups at Cataloochee Creek (Figs. 2.3, 2.5). Additionally, the algal assemblage of the ambient communities showed little variation among microhabitats at Cataloochee Creek; in fact, the 2 source samples actually overlapped in ordination space (Fig. 2.3A).

Chattooga River

Collection.—Two microhabitats with current regimes analogous to those of Cataloochee Creek were sampled at Chattooga River. *Blepharicera corniculata* ($n = 13$) and *B. similans* ($n = 9$) were collected from submerged bedrock in a chute (fast) where the free-stream current velocity was 250 cm/s. *Blepharicera separata* ($n = 20$) was collected from submerged rocks in a slow riffle where the free-stream current velocity was 95 cm/s.

Diet overlap.—Based on larval gut samples, the 2 microhabitats differed significantly (MRPP; $A = 0.28$, $p < 0.001$) and were distinguished primarily along axis 2 in the sample ordination (Fig. 2.4A). In addition, large, significant pairwise differences in the diets of groups that occurred in different microhabitats were detected (Table 2.5). Interhabitat differences reflect the disproportionately large biovolumes of the small, adnate diatom *A. minutissimum* in the diet of *B. separata*, which contrasted the large contributions of the small, chain-forming diatom *Fragilaria vaucheriae* and the rosette-forming diatoms *Synedra rumpens* and *Synedra* sp. cf. *ulna* to diets of *B. corniculata* and *B. similans* (Fig. 2.4B). A slight difference in the algal

assemblage structure of *B. corniculata* and *B. similans* gut samples was detected (Table 2.5)

and was attributable in part to the larger contribution of *A. minutissimum* to the diet of *B.*

similans (Fig. 2.4B).

Grazing efficiency.—Within the chute, the algal assemblage of *B. corniculata* and *B. similans*

guts showed an ~70% average Bray–Curtis similarity to that of the ambient algal community

(Fig. 2.5). The algal assemblage of larval *B. separata* guts, however, showed only a 30%

average Bray–Curtis similarity to that of the ambient algal community (Fig. 2.5). The low

grazing efficiency for *B. separata* was primarily attributable to the disproportionately large

contribution of *A. minutissimum* to larval guts relative to its availability on the substratum (Fig.

2.4B). At Chattooga River, *B. separata* ingested the highest algal biovolumes per individual

despite that their diet consisted primarily of the small diatom *A. minutissimum* (Fig. 2.5). In

fact, *B. separata* ingested the highest total number of diatom frustules per individual across all

sites.

Discussion

Grazing patterns of larval Blepharicera

Our findings corroborate previous reports that larval blepharicerids are scrapers that

feed almost exclusively on diatoms (Tonnoir 1930, Alexander 1963, Brodsky 1980, Georgian

and Wallace 1983, Dudley et al. 1990). Analysis of larval grazing efficiency often revealed a

substantial deviation in the algal assemblage of larval gut contents from that of the resource

base, and this deviation was not attributable to disproportionately low abundances of

understory taxa. In fact, one of the more striking findings of this study was the large

contribution of small, adnate diatoms to larval diets because the resistance of these taxa to

ingestion by grazers is well documented (Dickman 1968, Nicotri 1977, Peterson 1987,

Steinman *et al.* 1987). Peterson *et al.* (1998) suggested that algae in heavily grazed streams

face a trade-off between resistance to ingestion and resistance to digestion by invertebrate

grazers, noting the significantly higher percentages of dead ingestion-resistant species [e.g., *A. minutissimum* and *Cocconeis placentula* v. *euglypta* (Ehr.) Cl.] compared with dead ingestion-susceptible species (e.g., *Fragilaria* spp.). The higher percentages of dead cells of ingestion-resistant taxa were thought to be the result of repeated ingestion of those taxa by grazers (Peterson *et al.* 1998). The avoidance strategy (i.e., an adnate or prostrate growth form) of these taxa to ingestion apparently fails them under severe grazing pressure (Peterson *et al.* 1998) or in the presence of true scrapers (e.g., *Blepharicera*). The inaccessibility of these diatoms to grazers probably reflects constraints imposed by the grazer's mouthpart morphology (Steinman 1996, Peterson *et al.* 1998), so that any grazer possessing morphological adaptations that allow removal of understory diatom species has unusual access to highly digestible, high-quality food. Proportions of *Achnanthes sensu lato* species (e.g., *A. minutissimum*, *Achnanthes deflexa* v. *alpestris*, or *Achnanthes* sp. #5) and *Cocconeis placentula* v. *lineata*—species with growth habits that typically render them unavailable to grazers—were often higher in *Blepharicera* guts relative to their detected availability on the substratum. This overabundance of small, adherent growth forms in larval diets is somewhat unusual, and the ability of larval *Blepharicera* to harvest these taxa from the periphytic understory likely makes them excellent competitors within local guilds of stream grazers. Poff and Ward (1992) found that another scraper, *Agapetus* Curtis differentially ingested *Cocconeis placentula*. Our findings show that larval *Blepharicera* constitute a guild of highly specialized, true scrapers.

With the exception of a few intermittent patches of exposed bedrock, the cascade at Brasstown Falls was colonized entirely by aquatic bryophytes to the exclusion of immature *Blepharicera*. The gut contents of *B. similans* from the cascade, however, contained no trace of bryophytes. It is therefore conceivable that larvae subsisted on scattered patches of diatoms interspersed among the more pervasive bryophytes. The guts of the cascade-inhabiting *B. similans* group consisted primarily of the small diatom *Achnanthes* sp. #5, the medium-sized

diatoms *Fragilaria vaucheriae* and *Gomphonema* sp. #1, and the comparatively large diatom *Synedra* sp. cf. *ulna* (Table 2.2). The low algal biovolumes ingested by individuals from the cascade, therefore, does not reflect a diet of small, numerically abundant diatoms (Fig. 2.5); rather, they reflect a diet of average-sized, numerically depauperate taxa, which corroborates the patch-feeding hypothesis. Hart (1985b) noticed patches of diatoms interspersed among thicker macroalgal mats and found that *Leucotrichia* Mosely larvae subsisted entirely on and perhaps even maintained these preferred patches (or "lawns") of low-growing algae.

For our study, microhabitats were identified primarily by quantitative and qualitative variation in flow characteristics. At Cataloochee Creek and Chattooga River, free-stream current velocity distinguished "fast" and "slow" microhabitats, whereas qualitative differences in substratum exposure differentiated microhabitats at Brasstown Falls. Distribution patterns of larval *Blepharicera* within a system are undoubtedly affected directly by local variation in flow characteristics; however, the extent to which observed distributions also reflect history, competitive interactions (see below), or resource distribution is unknown. The spatial heterogeneity of food is well documented (Hart and Resh 1980, Hart 1981) and may be influenced by foraging activity of grazers (Hart 1981, McAuliffe 1984b). Microscale distribution of larval *Blepharicera* is probably affected to some extent by resource discontinuity or depression by congeners and deserves formal consideration in subsequent studies. Stevenson (1996) suggested that current can indirectly shape invertebrate distributions through its direct effect 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 affected ambient algal assemblages only in the absence of grazers. The effects of current on benthic algae are considered to be positive up to ~50 cm/s (Stevenson 1996), roughly half the velocity of slow microhabitats frequented by larval *Blepharicera* in this investigation. The fast and slow currents described in the literature are substantially slower than those reported in this study (Stevenson 1996 and references therein), hence extrapolation

of documented information to flow regimes encountered in this study is impossible.

Investigations into the effects of extreme current on the densities and distributions of

rheophilous algae and invertebrate grazers are a prerequisite to understanding the complex

relationships between the two groups (Poff and Ward 1995, Hart and Finelli 1999). In

addition to accounting for algal cell densities, reciprocally transplanting marked conspecifics

among microhabitats might afford insight into the effect of current velocity on larval grazing

patterns. Modification of our sampling technique to include estimation of microscale variation

in current velocity around individual rocks relative to larval and algal distribution rather than

simple estimation of free-stream current velocity for the entire microhabitat might have

increased the resolution of our data.

Isolation of congeneric species

The striking temporal and spatial overlap among larval *Blepharicera* species in the

southern Appalachian Mountains seems at odds with the basic tenets of competition theory. To

investigate this overlap, we have quantified the diets of larval congeners in the context of

admittedly crude microhabitat qualifications. We did not investigate competition per se, rather

we were interested in and hence examined resource overlap. Do larval congeners overlap in

their exploitation of food as they do in time and (less so) in space? Our collections were

carefully planned to maximize the probability of detecting dietary differences among congeneric

species that result from some mechanism of resource partitioning: First, 10 years of collection

data suggest that the greatest increase in absolute biomass occurs during the fourth (final) instar

larval stage (G. W. Courtney, unpublished data), consistent with documented data for *B.*

williamsae (Georgian and Wallace 1983). Second, for absolute numbers of diatom frustules,

fourth instars consume the most food (A. J. Alverson, unpublished data). In general, the

comparatively greater consumption of food by final-instar larvae compared with earlier instars

is well documented (Waldbauer 1968, Winterbourn 1971, Anderson and Grafius 1975, Hart

and Resh 1980). Otto (1971) and Anderson and Cummins (1979) emphasized larval

requirement of rich food sources during the final instar, and Hart and Resh (1980) hypothesized that increased food intake by final-instar larvae directly increases the Darwinian fitness of individuals. Third, phenological data for the southern Appalachian fauna reveal that the fourth-instar stadium of some taxa (e.g., *B. magna*) is much longer than earlier larval stadia, which might be interpreted as an enhanced ability of fourth instars to harvest and assimilate food. Fourth, all sampling occurred when leaf-out in southern Appalachia was complete, so stream exposure to sunlight was at an annual minimum, which may limit algal productivity at some sites. Finally, our sampling date should have occurred at a time when temporal overlap in the larval activity of congeners was the greatest. Collectively, these findings point to maximum exploitation of the forage base and maximum grazing pressure on the potentially limiting food supply by fourth-instar *Blepharicera* larvae. Thus, if larvae do in fact partition food, we have no reason to suspect that our collections should not reflect this partitioning.

Competition among grazers is presumed to be an important determinant of community structure and function in stream ecosystems (McAuliffe 1984a, Hart 1985a, Lamberti *et al.* 1987b, Dudley *et al.* 1990). Our findings suggest that mechanisms of spatial and phenological isolation among sympatric *Blepharicera* in southern Appalachia adequately reduce potential interspecific competition for food resources. Within a microhabitat, ecologically compatible groups effectively coexist, perhaps below some local carrying capacity. By partitioning the microhabitat, larval congeners concomitantly partition food. This partitioning is evidenced by the substantive, statistically significant interhabitat differences in larval diets and the large degree of dietary overlap among congeners that co-occurred within a microhabitat. A critical assumption of competition theory (that we made no effort to measure in this study) is that resources are available in limited supply (Birch 1957). Because of their habitat restrictions, space and food seem probable determinants of intra- and interspecific competitive interactions among immature blepharicerids. In western streams, Dudley *et al.* (1986) showed that larval

Blepharicera compete for space with macroalgae, and Dudley *et al.* (1990) clearly demonstrated that larval *Blepharicera* compete for space with larval *Simulium* Latreille. Competition for space with *Simulium* decreased total diatom ingestion in larval *B. micheneri* by 60% (abundance), resulting in inhibition of larval growth, increased time to pupation, increased mortality, and ultimately an ~50% decrease in *Blepharicera* secondary production (Dudley et al. 1990). Dudley *et al.* (1990) also detected significant inhibition of larval growth resulting from intraspecific competition among *B. micheneri* individuals; however, the effects of intraspecific competition were difficult to interpret because of competitive interactions with *Simulium*. In western North American streams, where blepharicerid diversity is considerably less than that of eastern North American streams, intra- and interspecific competition clearly impact blepharicerid populations. Thus, it seems likely that some of these same phenomena contribute to the structure of blepharicerid populations in eastern streams, where blepharicerids are considerably more diverse. Incidentally, larval black flies were relatively rare at our study sites during the sample period.

It also remains possible, even likely, that overlap in resource use (time, space, and food) among larval *Blepharicera* effectively narrows the ecological breadth of one, several, or all sympatric species. For example, in the central Appalachians, where *Blepharicera* diversity is considerably less than that in the southern Appalachians, *B. appalachiae* is essentially ubiquitous, occupying a broad range of current velocities and microhabitats (G. W. Courtney, unpublished data). In the southern Appalachians, where blepharicerid diversity is much greater, *B. appalachiae* is restricted to rocks in slow currents. The few *B. appalachiae* immatures that occupy faster currents were restricted to the less exposed surfaces and undersides of rocks. If these observations are accurate and are 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). Direct measurement of resource overlap alone is not sufficiently sensitive for detecting competition; in fact, species can

overlap in their use of several resources and not be competing (Menge 1979). The coexistence of sympatric *Blepharicera* might persist through sufficient divergence in some other relevant, though unmeasured, dimension or dimensions of the multidimensional niche space (Pianka 1975, Connell 1980).

Concluding remarks

We have integrated an entire suite of ecological factors and complex interactions among *Blepharicera* into a single collection at a given point in time: the simple collection of material has inherent bias. Interspecific interactions and grazing patterns reflect countless abiotic, biotic, and historical factors. The sum of these interactions is forced into some artificial context by simply collecting the material. Despite these limitations, we have quantitatively addressed blephacerid dietary characteristics as they relate to generalized patterns of larval distribution within streams. In doing so, we have clarified some poorly understood aspects of blephacerid life history and ecology.

Blephacerids can be an important component of lotic ecosystems. Data from this study confirm the role of larvae as grazers in both the sheer quantity of algae ingested and their unusual ability to harvest otherwise ingestion-resistant diatom species. This study is just one in a growing body of evidence emphasizing the importance of blephacerids in the trophic pathways of stream communities. High densities of larval grazers translate into substantive secondary production, and in turn, into important food resources for lotic fish. Newly afforded taxonomic resolution of the eastern *Blepharicera* will undoubtedly confirm the sensitivity of several species to stream quality. Because of unusual ecological characteristics, additional investigations into macro- and microscale distribution patterns of immatures relative to algal community structure and current velocity will facilitate our understanding of rheophilous community dynamics.

Acknowledgements ——

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Fig. 2.1. Scanning electron micrographs (SEM), Blephariceridae mouthparts, scale bar = 50 μm. Fig. 1A. *Blepharicera*

cherokea mouthparts; lrm, labrum; mxl, maxillae; lbm, labium; mnd, mandible. Figs 1B and 1C. SEM of Blephariceridae

mandibles showing lack of wear in a recently ecdysed larva (Fig. 1B) and worn mandibles due to scraping in a mature larva
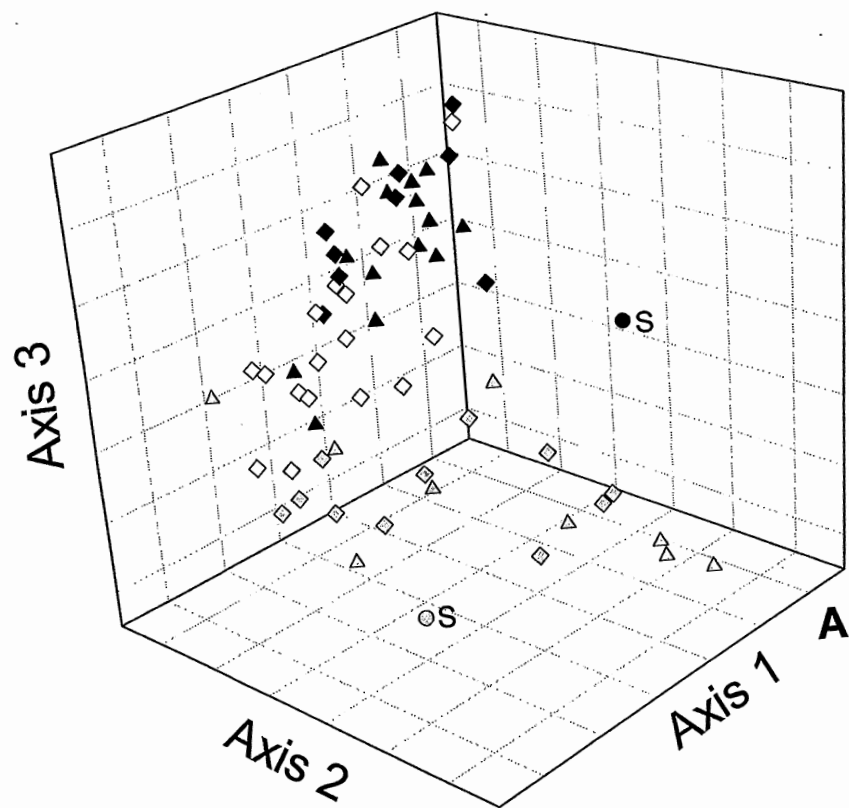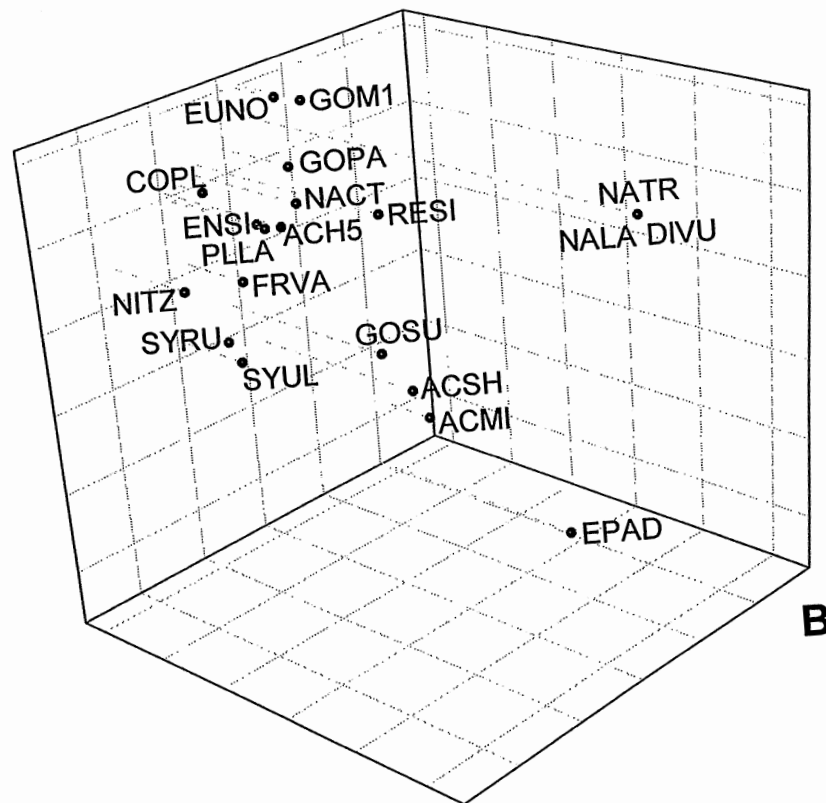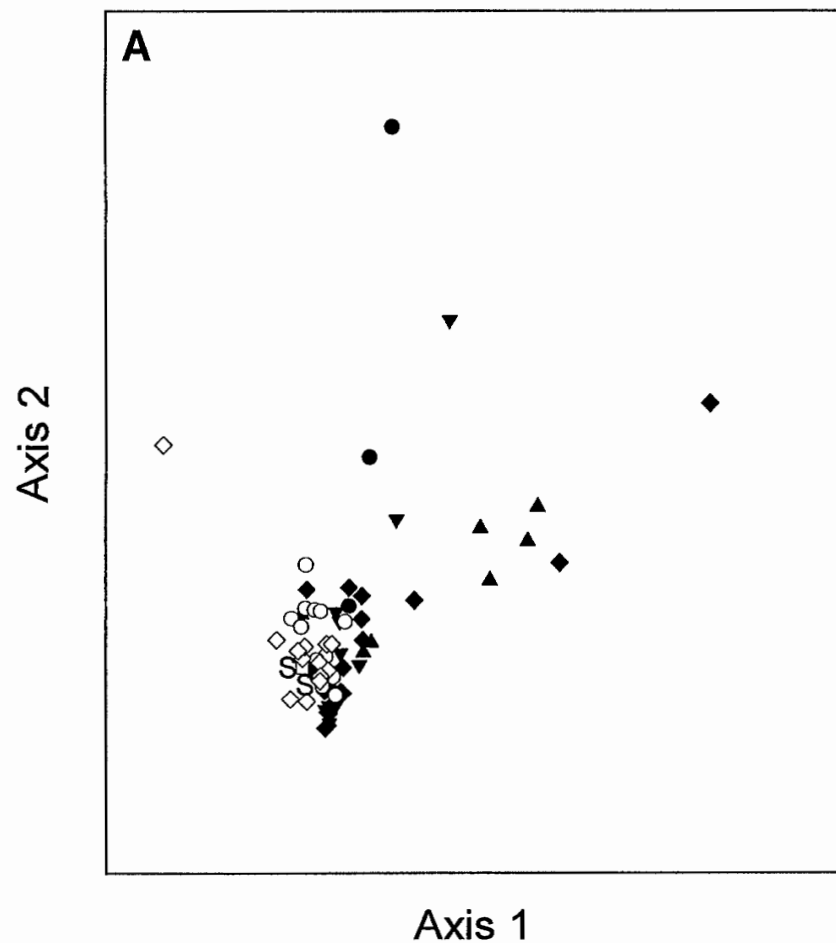
(Fig. 1C).
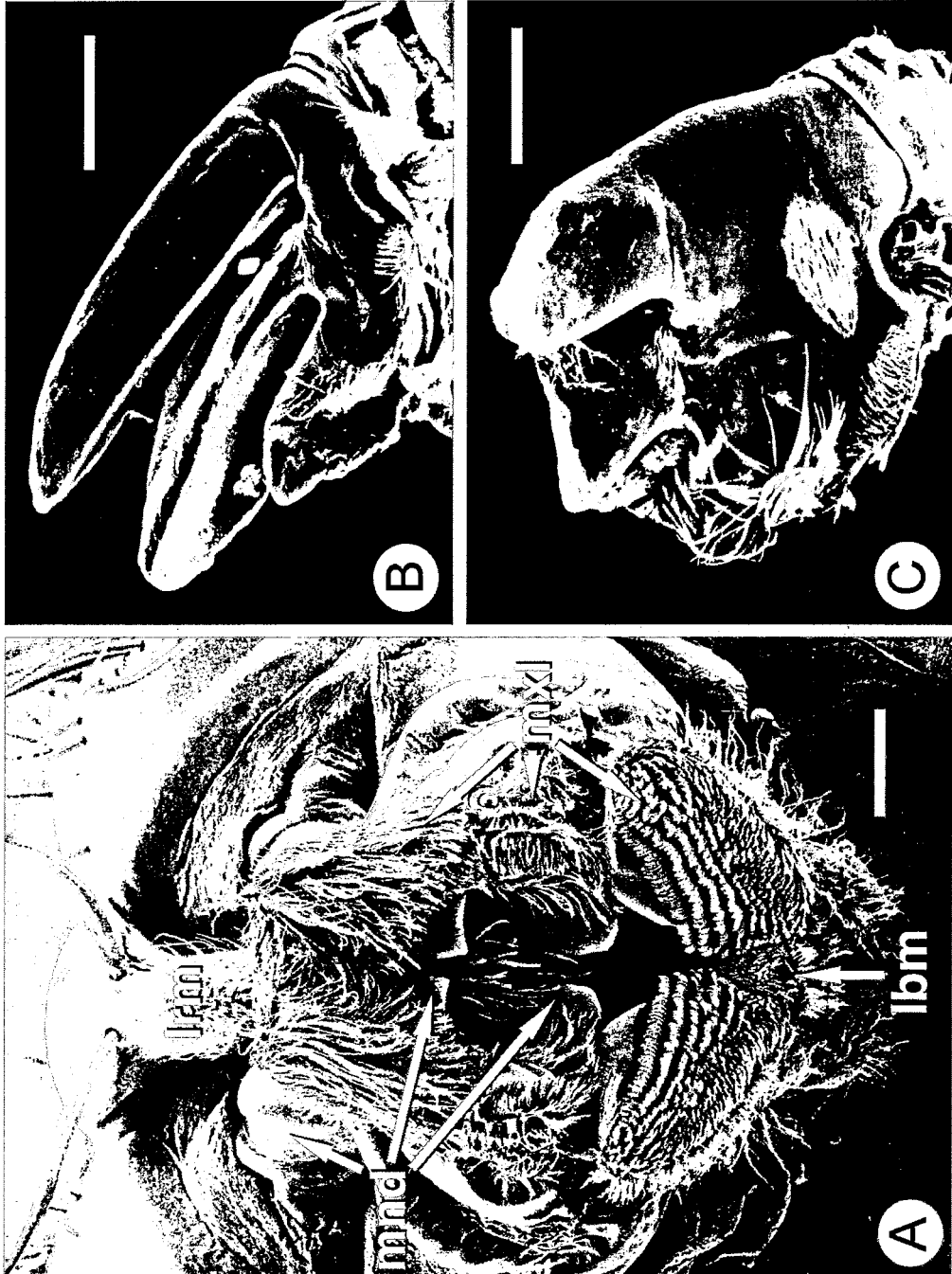
Fig. 2.2. (a) Three-dimensional NMDS plots of Bray-Curtis distances among larval gut and source samples from Brasstown Falls, South Carolina. Stress = 0.088. Symbols identify the sample: *B. diminutiva*, triangles; *B. similans*, diamonds; and Source (S), circles. Symbol pattern identifies the microhabitat: crash, gray; hygropetric, filled; cascade, open. (b) Three-dimensional species plot approximating the distribution of diatom taxa among samples (see Table 2.2 for abbreviations).
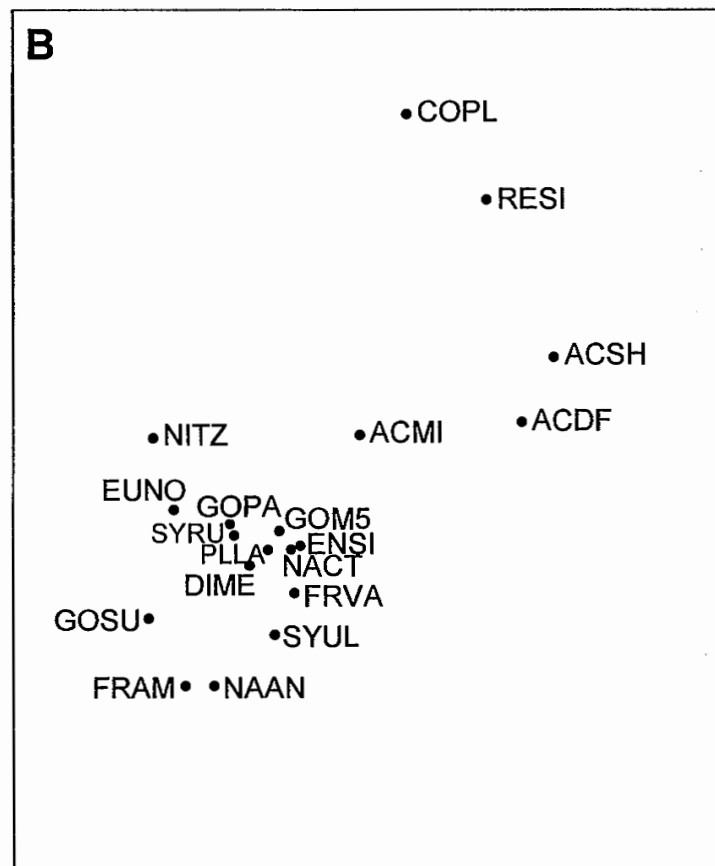
Brasstown Creek sample ordination

Species plot

EUNO GOM1
COPL GOPA
NACT
ENSI ACH5 RESI
PLLA
NITZ FRVA
SYRU
SYUL GOSU
ACSH
ACMI

NATR
NALA DIVU

EPAD

Axis 3
Axis 2
Axis 1

A

B

S

S

41

Fig. 2.3. (a) Two-dimensional NMDS plot of Bray-Curtis distances among larval gut and source samples from Cataloochee

Creek, North Carolina. Stress = 0.071. Symbols identify the sample: *B. appalachiae*, circles; *B. cherokea*, triangles (point

up); *B. similans*, diamonds; *B. tuberosa*, triangles (point down); Source (S), squares. Symbol pattern identifies the

microhabitat: fast, filled; slow, open. (b) Two-dimensional species plot approximating the distribution of diatom taxa among

samples (see Table 2.2 for abbreviations).
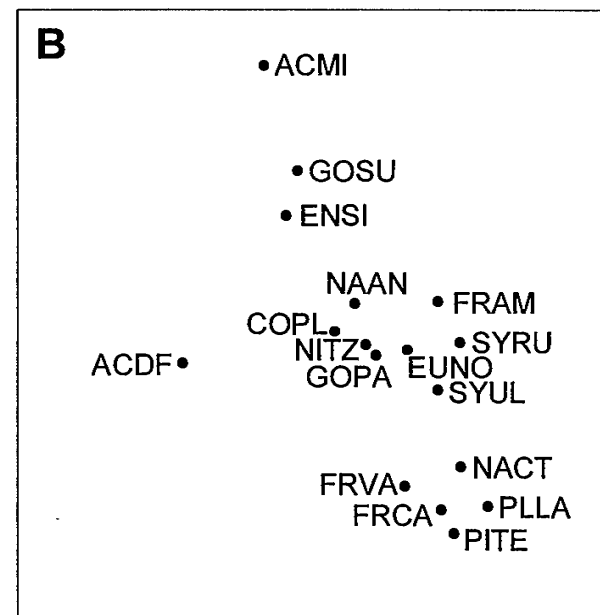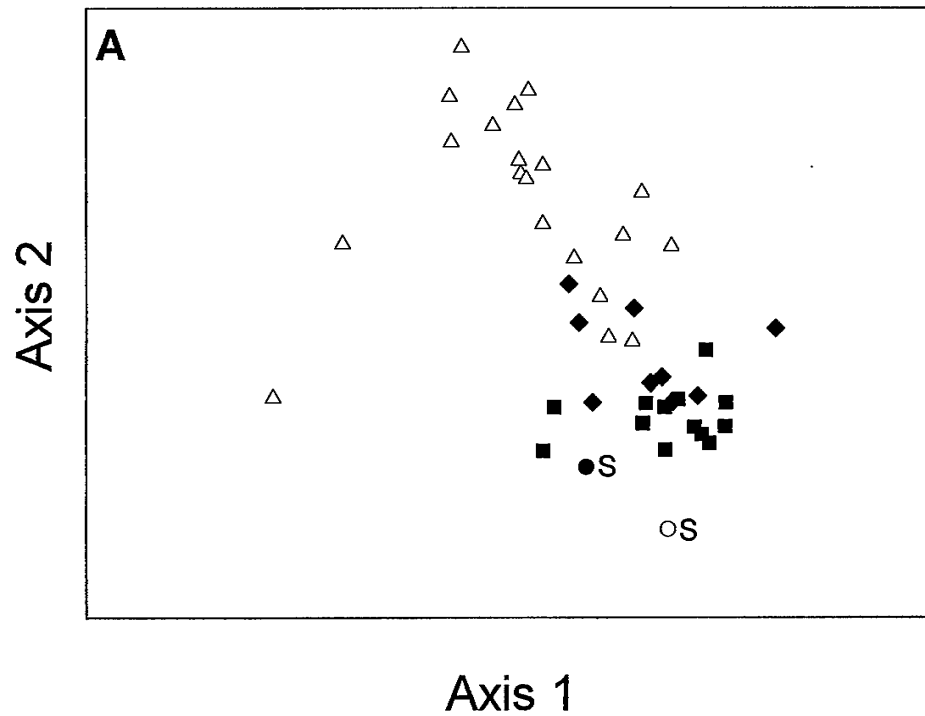
Cataloochee Creek sample ordination

Species plot

Axis 2

Axis 1

A

B

•COPL

•RESI

•ACSH

•ACDF

•NITZ   •ACMI

EUNO
•   GOPA GOM5
SYRU• • •ENSI
PLLA• •NACT
DIME   •FRVA

GOSU•

•SYUL

FRAM• •NAAN

Fig. 2.4. (a) Two-dimensional NMDS plot of Bray-Curtis distances among larval gut and source samples from Chattooga River, South Carolina. Stress = 0.084. Symbols identify the sample: *B. corniculata*, squares; *B. separata*, triangles; *B. similans*, diamonds; Source (S), circles. Symbol pattern identifies the microhabitat: fast, filled; slow, open. (b) Two-dimensional species plot approximating the distribution of diatom taxa among samples (see Table 2.2 for abbreviations).

Chattooga River sample ordination

A

Axis 2

●S

○S

Axis 1

Species plot

B

● ACMI

● GOSU
● ENSI

NAAN
● ● FRAM
COPL●
NITZ● ● ● SYRU
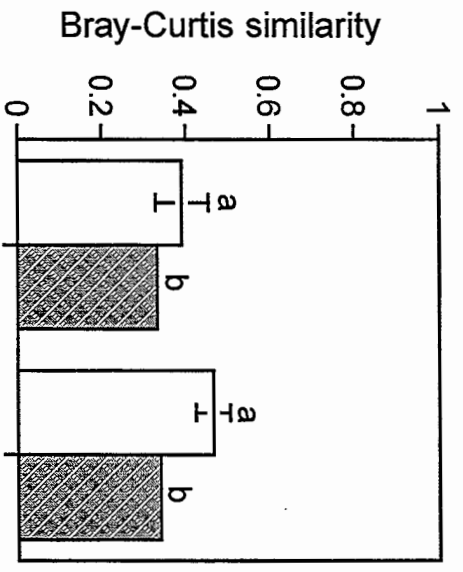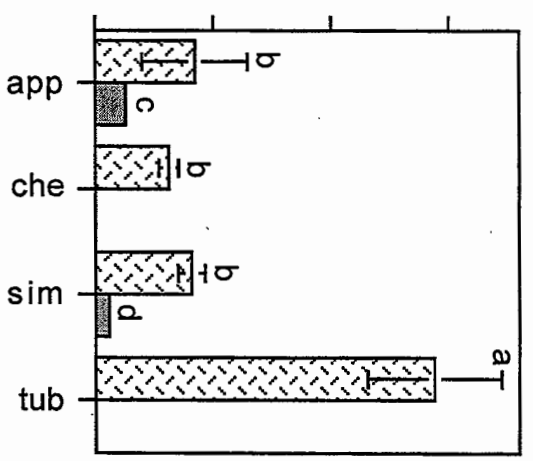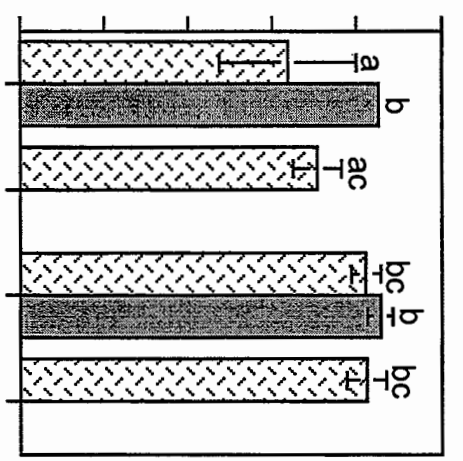GOPA EUNO
ACDF● ● SYUL

● NACT
FRVA●
FRCA● ● PLLA
● PITE

Fig. 2.5. Mean Bray-Curtis similarity (±1 SE) and mean algal biovolume ingested per individual (±1 SE) as measures of grazing efficiency among larval groups from 3 sites in the southern Appalachian Mountains. Within a graph, columns with similar labels do not differ significantly (p ≥ 0.04).
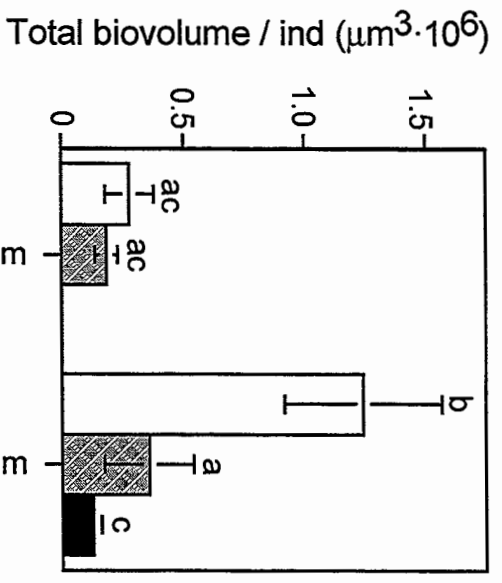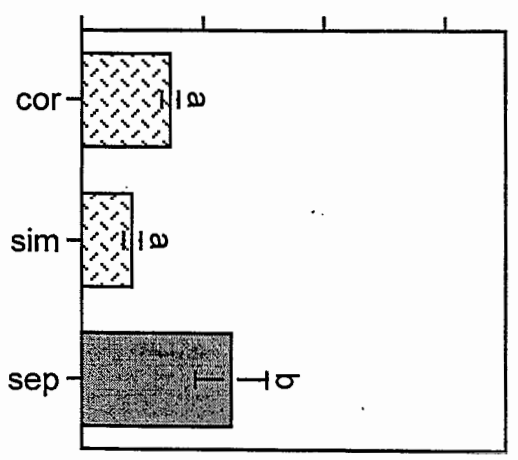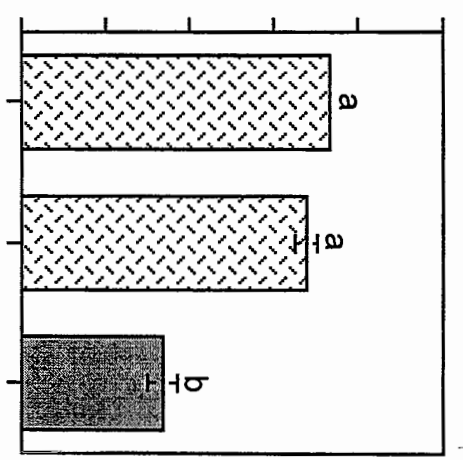
Table 2.1. Diversity and generalized patterns of ecological isolation of sympatric *Blepharicera* from Brasstown Falls (BF), Cataloochee Creek (CC), and Chattooga River (CR). Species codes identify species in figures and tables.

Species	Species code	Relative abundance			Season of larval growth	Current regime
		BF	CC	CR		
B. coweetae Hogue & Georgian	—	*	***	***	winter	H
B. magna Courtney	—	—	***	**	winter	H
B. williamsae Alexander	—	***	***	*	winter	H
B. capitata Loew	—	—	—	**	early spring	L
B. appalachiae Hogue & Georgian	app	—	***	***	spring	L
B. cherokea Hogue	che	***	***	**	spring	H
B. corniculata Courtney	cor	—	—	**	spring	H
B. tuberosa Courtney	tub	—	***	—	spring	H

Data based on collections from 1990 to 1999. ***, common; **, uncommon; *, rare; —, absent; L, low; M, medium; H, high.

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Table 2.1. (continued)

Species	Species code	Relative abundance			Season of larval growth	Current regime
		BF	CC	CR		
B. separata Alexander	sep	*	**	***	early summer	L
B. chattooga Courtney	—	—	—	***	summer	L
B. diminutiva Hogue	dim	***	—	*	summer[a]	hygropetric
B. similans Johannsen	sim	***	***	***	summer–fall[a]	M

[a] Possibly multivoltine

Table 2.2 Characteristics of the 27 most common diatom taxa from the diets of larval *Blepharicera* at Brasstown Falls (BF), Cataloochee Creek (CC), and Chattooga River (CR). Species codes identify taxa in figures.

Species	Species code	Growth habit	Estimated biovolume ($\mu m^3 \cdot$ frustule^{-1})	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 sp. cf. *ulna*	SYUL	rosette-forming	1124	+	+	+
Fragilaria vaucheriae (Kütz.) Peters.	FRVA	chain-forming	239	+	+	+
Cocconeis placentula 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	+	+	−

Table 2.2. (continued)

Species	Species code	Growth habit	Estimated biovolume ($\mu m^3 \cdot$ frustule^{-1})	Presence / absence in samples		
				BF	CC	CR
Achnanthes sp. #5[a]	ACH5	adnate?	69	+	−	−
Planothidium lanceolatum (Bréb) Round & Bukhtiyarova	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	+	−	−

[a] Probably *Rossithidium* Round & Bukhtiyarova sp.

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Table 2.2. (continued)

Species	Species code	Growth habit	Estimated biovolume ($\mu m^3 \cdot$ frustule^{-1})	Presence / absence in samples		
				BF	CC	CR
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) Mann	ENSI	mucilagenous tube- / mat–forming	157	+	+	+
Gomphonema parvulum (Kütz.) Kütz.	GOPA	pedunculate	237	+	+	+

Table 2.2. (continued)

Species	Species code	Growth habit	Estimated biovolume ($\mu m^3 \cdot$ frustule^{-1})	Presence / absence in samples		
				BF	CC	CR
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	+	+	+

Table 2.3. Results of MRPP for intra- and interhabitat comparisons of algal assemblages that comprised the diets of larval groups at Brasstown Falls, SC (see Table 2.1 for abbreviations). Post Bonferroni-corrected type I error rate was $\alpha' = 0.005$.

		crash zone		hygropetric		cascade
		dim	sim	dim	sim	sim
crash zone	dim	—	$A = -0.004$ $p = 0.45$	$A = 0.27$ $p < 0.0001$	$A = 0.28$ $p < 0.0001$	$A = 0.21$ $p < 0.0001$
	sim	—	—	$A = 0.26$ $p < 0.0001$	$A = 0.27$ $p < 0.0001$	$A = 0.19$ $p < 0.0001$
hygropetric	dim	—	—	—	$A = -0.005$ $p = 0.31$	$A = 0.07$ $p < 0.01$
	sim	—	—	—	—	$A = 0.10$ $p < 0.001$

Table 2.4. Results of MRPP for intra- and interhabitat comparisons of algal assemblages comprising the diets of larval groups at Cataloochee Creek, NC (see Table 2.1 for abbreviations). Post Bonferroni-corrected type I error rate was $\alpha' = 0.003$.

| | | fast | | | | slow | |
		app	che	sim	tub	app	sim
fast	app	—	$A = 0.02$ $p = 0.24$	$A = 0.02$ $p = 0.18$	$A = 0.01$ $p = 0.34$	$A = 0.05$ $p = 0.02$	$A = 0.07$ $p < 0.01$
	che	—	—	$A = 0.10$ $p < 0.01$	$A = 0.12$ $p < 0.01$	$A = 0.20$ $p < 0.001$	$A = 0.20$ $p < 0.001$
	sim	—	—	—	$A = -0.02$ $p = 0.84$	$A = 0.06$ $p < 0.01$	$A = 0.05$ $p < 0.01$
	tub	—	—	—	—	$A = 0.06$ $p = 0.01$	$A = 0.04$ $p = 0.01$
slow	app	—	—	—	—	—	$A = 0.03$ $p = 0.04$

Table 2.5. Results of MRPP for intra- and interhabitat comparisons of algal assemblages comprising the diets of larval groups at Chattooga River, SC (see Table 2.1 for abbreviations). Post Bonferroni-corrected type I error rate was $\alpha' = 0.017$.

		slow	fast	
		corn	sim	sep
fast	corn	—	$A = 0.055$ $p < 0.01$	$A = 0.31$ $p < 0.0001$
	sim	—	—	$A = 0.18$ $p < 0.0001$

CHAPTER 3. TEMPORAL PATTERNS OF DIATOM INGESTION BY LARVAL NET-WINGED MIDGES (DIPTERA: BLEPHARICERIDAE: *BLEPHARICERA* MACQUART) FROM GREAT SMOKY MOUNTAINS NATIONAL PARK, NORTH CAROLINA

An article to be submitted to Freshwater Biology

Andrew J. Alverson[1] and Gregory W. Courtney[1]

Abstract. Eight *Blepharicera* species inhabit Cataloochee Creek, North Carolina. Based on season of larval activity, species can be broadly distinguished as winter, spring, or summer types. We examined fourth-instar diets of 2 temporally isolated species that have relatively long larval activity periods and a protracted fourth-instar stadium. Dietary assemblage structure, larval grazing efficiency, and total diatom consumption were measured for *B. magna* (winter type) and *B. similans* (summer type) to investigate whether larval grazing patterns changed over time. Data showed that algal assemblages in diet of *B. magna* did not vary over time. Algal assemblages in the diet of *B. similans* varied significantly throughout its fourth-instar stadium. Furthermore, for both species, total diatom consumption was greatest at midstage, and both species showed consistently low larval grazing efficiency due to positive differential ingestion of diatom species with adnate and prostrate growth forms.

Introduction

Net-winged midges are a common and often important component of lotic community assemblages in western and eastern North American streams. Larvae are rheophilic specialists, inhabiting cascades, waterfalls, and torrential streams. The four larval instars are distinctive, characterized by morphological adaptations to rheophily. The fusion of head, thorax, and abdominal segment I into a single, compact division (= cephalothorax) keeps the anterior body within a viscous region of the boundary layer. In addition, the possession of 6 ventral

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[1] Iowa State University, Department of Entomology, 407 Science II, Ames, Iowa 50011

suctorial discs ensure attachment to substrata and render larvae among the most well-adapted of the torrenticolous insects. Pupae are also well-adapted for life in swift flow, being dorsoventrally compressed, nearly perfectly streamlined [though see Pommen and Craig (1995)], and cemented immovably to substrata via a series of ventrolateral abdominal pads.

Recent taxonomic and descriptive work has revealed that the Appalachian Mountains are home to the highest diversity of Blephariceridae in North America, with 16 species of *Blepharicera* Macquart inhabiting the region (Courtney 2000). The southern Appalachians are particularly diverse, with 13 of these species (Courtney 2000). The result is a high degree of regional and local sympatry that challenge fundamental tenets of competition theory, especially in light of the group's restricted habitat requirements. Spatial and dietary segregation of coexisting *Blepharicera* species from 3 sites in southern Appalachia was the subject of investigation by Alverson *et al.* (2000). This study showed no strong evidence for partitioning of food resources among congeners where spatial overlap was most acute (i.e., within a microhabitat), suggesting that mechanisms of temporal and spatial isolation of sympatric *Blepharicera* might sufficiently minimize interspecific competition for food.

Phenological isolation of sympatric species is well documented for several groups of stream invertebrates (Wallace and Anderson 1996 and references therein), including Blephariceridae (Kitakami 1950, Zwick 1977, Zwick 1980, Georgian and Wallace 1983, Courtney 2000). Based on larval activity period, Kitakami (1950) distinguished Japanese species as winter, summer, or perennial types. Winter types were further classified into either of 2 univoltine subtypes: First subtype (early) species hatch in September or October, overwinter as fourth instars, pupate in April, and emerge in May (Kitakami 1950). Second subtype (late) species have shorter larval activity periods, with eggs hatching in December or later (Kitakami 1950). Summer-types were also subdivided into 2 types: first subtype (early) species are univoltine, hatching in May or June, pupating in July or August, and emerging in August (Kitakami 1950). Second subtype (late) species are bivoltine, with first generation

larvae hatching in early to mid-Spring, second generation larvae hatching some time later, and both generations emerging in autumn (Kitakami 1950). Subsequent life cycle classifications have been variants of the Kitakami (1950) scheme, including those of Italian and Corsican faunas (Zwick 1980), western Nearctic fauna (Courtney 1991), and the more rigorous classification of the Australian fauna (Zwick 1977). Johns (1996) and Courtney (2000) classified Appalachian species as winter, spring [= late winter type of Kitakami (1950)], or summer types. Most investigators consider temporal partitioning to reflect the interrelationship of temperature and season (Kitakami 1950, Zwick 1977, Courtney 1991). Life-cycle characteristics of *Blepharicera* species at our study site are summarized in Table 3.1.

Alverson *et al.* (2000) documented larval diets of 7 *Blepharicera* species collected in late spring and confirmed that Appalachian *Blepharicera* feed almost exclusively on epilithic diatoms. In this article, we report larval grazing patterns of 2 *Blepharicera* species over a period of several months. Cataloochee Creek, North Carolina, is home to 8 *Blepharicera* species; on the basis of season of larval activity, each species can be categorized broadly as either winter, spring, or summer type (Table 3.1). We tracked changes in fourth-instar diets of 2 temporally isolated species. We chose species that have relatively long larval activity periods and a protracted fourth-instar stadium, which precluded spring type species (Johns 1996, Courtney 2000). *Blepharicera magna* is a univoltine, early winter type species with an exceptionally long larval activity period, spanning from September through March (Table 3.1); the first three stadia are brief, and by October, fourth instars begin to appear. *Blepharicera magna* overwinters as mature fourth instars and typically emerge in April or May (Courtney 2000). *Blepharicera similans* is a univoltine, late summer type species with a larval activity period spanning at least from June through August—fourth instars have also been collected from Cataloochee Creek in May and September (A. J. Alverson and G. W. Courtney, unpublished data). *Blepharicera similans* usually emerges in late summer (Courtney 2000).

Temporal patterns of macroinvertebrate grazing are well documented for insect grazers in laboratory streams and for freshwater snails in laboratory and natural streams. Lamberti *et al.* (1987), Steinman *et al.* (1987), and DeNicola *et al.* (1990) monitored relatively long (48 d, 32 d, and 40 d, respectively) temporal trends in the interactions of 2 or 3 functionally different macroinvertebrate grazers with periphyton assemblages. The aforementioned were conducted in laboratory streams, and grazing was monitored by measuring parameters of the ambient algal communities (e.g., algal biomass, assemblage structure, chlorophyll *a*), rather than by direct assessment of macroinvertebrate dietary assemblages (Lamberti *et al.* 1987, Steinman *et al.* 1987, DeNicola *et al.* 1990). Hunter (1980) conducted a similar 45 d field experiment with 3 grazing snails, again opting to assess temporal grazing patterns by monitoring changes in various parameters of the ambient algal community. Dillon and Davis (1991) examined diatom ingestion by 3 species of coexisting snails from 4 dates and noted seasonal changes in dietary assemblages. Georgian and Wallace (1983) tracked seasonal patterns of secondary production in a guild of stream grazers from a southern Appalachian stream and clearly demonstrated temporal separation of *B. williamsae* Alexander and "*Blepharicera* spp." (a composite of ≥2 species). Georgian and Wallace (1983) also showed that secondary production is highest for *B. williamsae* at the end of its larval activity period. General dietary patterns throughout larval life history have been documented for several groups. Net increases in total food consumption have been observed in final instars of several insect groups (Waldbauer 1968, Winterbourn 1971, Anderson and Grafius 1975); furthermore, Otto (1971), Winterbourn (1971), Anderson and Cummins (1979), and Hart and Resh (1980) have emphasized larval requirement of higher quality food resources during the final instar.

In this study, we examined temporal dietary patterns at a slightly different scale than those of previous investigations. We report on temporal changes in the fourth-instar diets of 2 phenologically isolated insect scrapers, *B. magna* and *B. similans*, from Cataloochee Creek, NC. We document monthly changes in larval dietary assemblages, larval grazing efficiency

sensu Peterson *et al.* (1998), and total diatom consumption to elucidate potential fluctuations in larval grazing patterns over time.

Methods

Cataloochee Creek (35°40′N, 83°04′W) is a fourth order stream in the Tennessee River basin that drains the southeast sector of Great Smoky Mountains National Park, NC. 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].

Cataloochee Creek was sampled monthly from September 1998 through September 1999. Sampling was done at midday [1300–1700 hours (EST)] to eliminate the potential complication of fluctuating diurnal feeding rates. Because blepharicerid distribution within streams is usually nonrandom, sampling was based primarily on the presence of larvae and was, therefore, nonrandom. In essence, our samples represent ideal *Blepharicera* habitat. Each month, 2 or 3 rocks were randomly selected from a uniform riffle, and all noticeable larvae were removed with forceps and preserved in 6:3:1 (95% ethanol:water [collection]:10% formalin) solution. Ambient algae were then removed with a toothbrush and preserved in 6:3:1 solution. Algae were collected from areas corresponding with larval distribution on substrata. Although this collection method impeded cell density estimates, it was intended to minimize the impact that potentially aberrant diatom patches falling outside of the immediate larval grazing pasture had on estimation of ambient community structure. For each month, larvae and algae were pooled into composite samples of each. Throughout this article, individual larvae and ambient (source) algal collections are referred to as samples, and the sum of larval conspecifics from a single date are referred to as groups.

Laboratory preparation and analyses

At present, no keys are available for early instars of *Blepharicera*, so we examined only fourth-instar larvae. Ten individuals per month were examined. Prior to dissection, body length and head capsule width of each larva were recorded. The entire gut was removed with forceps 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 by using the mounting medium Naphrax. A subsample of each algal collection was acid-cleaned according to Patrick and Reimer (1966), air dried onto a coverslip, and slide-mounted by using Naphrax. All samples were examined at 600× with a Nikon E800 compound microscope. At least 1000 diatom valves per sample were randomly identified and enumerated using standard taxonomic references (Hustedt 1930, Patrick and Reimer 1966, 1975, Krammer and Lange-Bertalot 1991a,b, Krammer and Lange-Bertalot 1997a,b) and various floristic studies of the diatom species from the southeastern United States (Camburn and Lowe 1978, Kociolek 1982, Lowe and Kociolek 1984). Slides were then scanned to record rare taxa. If a gut sample consisted of <1000 diatom valves, the entire slide was counted. Valves rather than frustules were counted to account for potential differences in propensity of diatom taxa to separate from an intact frustule into valves. At least one-half of a valve had to be present to be included in the counts. Diatom images for major taxa are available in Alverson (2000). Raw counts were standardized by conversion to proportions of the total (i.e., relative abundances).

Statistical analyses

Dietary assemblages.—Gut and source samples were ordinated on the basis of the most common diatom species (i.e., those taxa that comprised an average of ≥2% of the total cells counted for at least one larval group or source sample—see Table 3.2) with correspondence analysis (CA, Hill 1973). Correspondence analysis is an eigenanalysis method used to represent similarity in species composition of samples (e.g., larval gut and source samples).

Interpoint distances in ordination plots show the degree of similarity among those samples, so that the greater the distance between 2 points in ordination space, the greater the dissimilarity of algal assemblages of the 2 samples. Winter and summer samples were analyzed independently.

Mantel permutation tests (Mantel 1967) were used to explore differences in the dietary assemblages of different larval groups. In this analysis, the null hypothesis of no linear correlation between 2 distance matrices (matrix X and Y) was tested. All intra- and interspecific pairwise group comparisons were tested. First, the Bray–Curtis dissimilarity metric was used to transform a data matrix of n larval gut samples by p diatom species into a triangular distance matrix, matrix X). Matrix Y was a design matrix set up to depict the alternative hypothesis, the existence of dietary differences between the 2 groups (Sokal and Rohlf 1995, Legendre and Legendre 1998). Subjecting two such matrices to the Mantel procedure is equivalent to performing a nonparametric multivariate analysis of variance (Sokal et al. 1993, Legendre and Legendre 1998). Hudon and Lamarche (1989) used this approach successfully to distinguish differences in use of food resources by coexisting American lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*). Mantel tests were performed with 9999 randomized runs to obtain the distribution for the test statistic; probability (p) value and standardized Mantel statistic (r) are presented for each comparison. Mantel tests and correspondence analysis were run with PC-ORD (version 4; MjM Software Design, Gleneden Beach, Oregon).

Grazing efficiency.—Grazing efficiency was assessed with the Bray–Curtis measure of similarity (Bray and Curtis 1957). The mean Bray–Curtis similarity between the algal assemblages of larval guts and that of the forage base was calculated for each larval group. The Bray–Curtis similarity ($S_{l,s}$) between the diatom assemblage of a larval gut (l) and its corresponding source sample (s) is given by

$$S_{l,s} = 1 - \frac{\sum_{j=1}^{p} |X_{l,j} - X_{s,j}|}{\sum_{j=1}^{p} (X_{l,j} + X_{s,j})}$$

for which $X_{l,j}$ and $X_{s,j}$ equal the relative abundance of diatom j in the larval gut and source

sample, respectively, and p equals the number of diatom taxa being compared. The equation

returns a proportion coefficient ranging from 0 (dissimilar) to 1 (similar) (Krebs 1989). The

Bray–Curtis metric weighs abundant dietary attributes more heavily than rare ones, is

insensitive to joint absences, and is generally regarded as a stable, well-behaved distance

measure (Field *et al.* 1982, Faith *et al.* 1987, Boyle *et al.* 1990). Interpoint distances between

larval gut and source samples in ordination space provide a visual approximation of larval

grazing efficiency.

  Chesson's alpha (α) (Chesson 1978) is an electivity index that was used to assess the

deviation in the proportions of particular dietary items from their proportions on the

substratum. Chesson's α is calculated by using the following equation:

$$\alpha = (r_i / p_i) / \sum (r_i / p_i)$$

for which r_i equals the relative abundance of diatom species i in the diet and p_i equals the

relative abundance of diatom species i in algal source sample. The index returns a proportion

coefficient ranging from 0 to 1, with values exceeding $1/n$ indicating larval "preference" for that

item and values less than $1/n$ indicating "avoidance" of that item, where n is the number of

diatom species included in the analysis. Chesson's α values were transformed by subtracting

$1/n$ from the index value (Peterson *et al.* 1998). Transformed values were then analyzed for

difference from zero using *t*-tests. Experimentwise type I error rate was maintained with

sequential Bonferroni corrections (Scheiner 1993).

Total diatom cells ingested per individual also was estimated and compared among larval groups. These estimates were made by consideration of total number of diatom valves enumerated, number of fields analyzed, field diameter, and total area.

A 1-factor analysis of variance (ANOVA) was used to assess differences in Bray–Curtis similarity coefficients. Analysis of variance with larval body length as a covariate was used to assess differences in estimates of total diatom ingestion among larval groups. Because estimates of the ambient algal community were based on 1 sample, they were excluded from all inferential statistical methods, including Mantel tests. 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 group comparisons were made with 2 sample t-tests, with the least squares means (LSMEANS) statement in the GLM procedure. For Mantel tests and ANOVAs, the Bonferroni method was used to maintain an experimentwise type I error rate of $\alpha = 0.05$, but because of the extremely conservative nature of the Bonferroni method and the arbitrariness of choosing the initial $\alpha = 0.05$, some potentially important effects that lack statistical significance are presented.

RESULTS

Blepharicera magna

Collection.—Larvae and algae from 3 dates were examined: 29 October 1998, 24 November 1998, and 21 December 1998. The collection dates span the first 3 months of the fourth-instar stadium of *B. magna* in typical years (Courtney 2000). High water prevented sampling in January, and no samples were taken in February. By March, larvae were prepupal. Analysis of prepupal guts confirmed previous observations that *Blepharicera* discontinue feeding and empty their guts prior to larva–pupa molts.

Dietary and ambient algal assemblages.—Ordination of larval *B. magna* gut samples and ambient algal samples from October, November, and December revealed several important

findings. Ambient algal samples from the 3 winter months are distinguished primarily along axis 1 in the CA sample ordination (Fig. 3.1a); from October through December, decreasing relative abundance of *Synedra rumpens* and increasing relative abundance of smaller, adnate and prostrate diatom taxa (i.e., *Achnanthes deflexa* v. *alpestris*, *A. subhudsonis* v. *kraeusellii*, *Achnanthidium minutissimum*, and *Cocconeis placentula* v. *lineata*) account for much of the displacement of algal samples in ordination space (Fig. 3.1). *Blepharicera magna* gut samples from the 3 winter months overlapped broadly in CA ordination space (Fig. 3.1a) and did not differ significantly (Table 3.3). Furthermore, the diffuse arrangement of each month's larval samples in ordination space demonstrates the ranging importance of *A. deflexa* v. *alpestris* and *Fragilaria vaucheriae* v. #1 in larval diets (Fig. 3.1).

Grazing efficiency.—Algal assemblages of *B. magna* guts from the 3 winter months showed an ~50% average Bray–Curtis similarity to that of the corresponding ambient algal community (Fig. 3.2a). Larval grazing efficiency did not vary significantly over the 3 winter months (Fig. 3.2a).

Chesson's α values for common diatom species showed which taxa influenced the moderately low larval grazing efficiencies that were detected with the Bray–Curtis similarity metric and were evident in the displacement of larval gut samples from source samples in ordination space. For October and November, the adnate diatom *A. deflexa* v. *alpestris* and the chain-forming diatom *F. vaucheriae* v. #1 had high α values, indicating the large relative abundance of these 2 species in larval diets compared with expectation (Fig. 3.3). In addition, several taxa were less abundant in larval diets than expected (Fig. 3.3).

Total diatom cell consumption for *B. magna* was substantially higher in November and December compared with that in October (Fig. 3.2b). Although differences were not significant, a discernable trend exists (Fig. 3.2b).

Blepharicera similans

Collection.—Larvae and algae from 3 dates were examined: 05 June 1999, 07 July 1999, and 13 August 1999. These dates spanned the entire fourth-instar stadium for *B. similans*. The larval activity period of *B. similans* is apparently somewhat plastic compared with those of congeners, with fourth instars having been collected in both May and September at Cataloochee Creek in the past (A. J. Alverson and G. W. Courtney, unpublished data).

Dietary and ambient algal assemblages.—CA ordination of larval *B. similans* gut samples and ambient algal samples from June, July, and August showed several important results. *Achnanthes deflexa* v. *alpestris* and *C. placentula* v. *lineata* were numerically dominant in summer algal samples, though the 3 samples are distinguished along axis 1 in the sample ordination (Fig. 3.4a). In July, a large increase in the relative abundance of *C. placentula* v. *lineata* (an increase clearly associated with a sexual reproductive event of that species) differentiated the July algal sample from those of June and August (Fig. 3.4a). Algal assemblages in the diets of *B. similans* varied significantly over the 3 summer months (Table 3.3). June samples were the least distinct of the 3 summer months, their arrangement in ordination space being noticeably diffuse (Fig. 3.4a). *Achnanthes deflexa* v. *alpestris* and *S. rumpens* were the most abundant taxa in larval diets from June, though the 2 comprised an average of only ~40% of the total diet (Table 3.2). Larval gut samples from July were virtually indistinguishable along axis 1, with their separation along axis 2 showing the relative importance of *A. deflexa* v. *alpestris*, *A. minutissimum*, and *C. placentula lineata* in larval diets (Fig. 3.4). Together, these 3 species accounted for an average of >90% of larval diets in July (Table 3.2). August gut samples were dominated by *A. deflexa* v. *alpestris*, *A. minutissimum*, and *C. placentula* v. *lineata*, though greater consumption of *A. subhudsonis* v. *kraeusellii* and several minor taxa differentiated August gut samples from those of the 2 previous month's (Fig. 3.4).

Grazing efficiency.—Algal assemblages of *B. similans* guts from the 3 summer months showed an ~50% average Bray–Curtis similarity to that of the corresponding source sample

(Fig. 3.5a). Larval grazing efficiency did not vary significantly over the 3 summer months (Fig. 3.5a).

Chesson's α values for common diatom species showed that in June, moderately low larval grazing efficiency was primarily attributable to positive differential ingestion of *A. deflexa* v. *alpestris*, *F. vaucheriae* v. #1, and *G. parvulum* (Fig. 3.6). In July, 3 diatom species with adnate or prostrate growth forms had high α values, whereas the remaining taxa (i.e., mostly larger stalked, chain, and rosette-forming diatoms) were less common in larval diets than expected (Fig. 3.6). In August, *A. deflexa* v. *alpestris* and *F. vaucheriae* v. #1 had high α values, and several minor taxa were less common in larval diets than expected (Fig. 3.6).

For *B. similans*, total diatom cell ingestion was significantly higher in July than it was in June and August (Fig. 3.5b).

DISCUSSION

Fourth-instar *Blepharicera* in southern Appalachian streams feed almost exclusively on epilithic diatoms. Georgian and Wallace (1983) studied seasonal production dynamics of several *Blepharicera* species from a southern Appalachian stream and noted that larval guts were full of "small diatom frustules." Dudley *et al.* (1990) found that larval diets of *B. micheneri* Alexander from a western North American stream consisted primarily of diatoms. Alverson *et al.* (2000) documented dietary assemblages of 7 *Blepharicera* species from 3 sites in southern Appalachian streams, also noting that diatoms dominated larval gut contents. Due in part to high lipid content, diatoms are a food resource of high nutritional value for macroinvertebrate grazers (Anderson and Cummins 1979, Round *et al.* 1990). Furthermore, some evidence suggests that diatoms are more easily digested and assimilated than bacteria and other algae (Kajak and Warda 1968, Hargrave 1970).

Data presented in this article demonstrate the high ingestion efficiency of *Blepharicera* for what are otherwise understood to be "grazer-resistant" species (e.g., *Cocconeis*, *Achnanthes*, *Achnanthidium*, and *Planothidium* species). Small size in conjunction with adnate or prostrate growth form renders these diatom taxa less susceptible to ingestion by most macroinvertebrate grazers (Dickman 1968, Nicotri 1977, Peterson 1987, Steinman *et al.* 1987). Poff and Ward (1992) found that *Agapetus* Curtis exhibited positive differential ingestion for the prostrate diatom *Cocconeis placentula* Ehr. Alverson *et al.* (2000) noted similar patterns of ingestion efficiency for grazer-resistant diatom species in several other Appalachian *Blepharicera* and suggested that ease of ingestibility of these taxa was attributable to highly specialized mouthparts. *Blepharicera* scrape substrata with large mandibles, enabling extraction of food particles from all layers of periphyton, including the understory (Courtney 1990, Alverson *et al.* 2000). Under instances of high grazing pressure, populations of grazer-resistant diatom taxa (i.e., species with adnate or prostrate growth forms) can have higher percentages of dead cells than taxa that are more susceptible to grazer ingestion (i.e., chain-forming *Fragilaria* species residing in the periphytic canopy) (Peterson *et al.* 1998). Peterson *et al.* (1998) suggested that high percentages of dead cells resulted from repeated ingestion by grazers, and that ultimately algae under sustained, high grazing pressure face a tradeoff between resistance to ingestion and digestion by macroinvertebrate grazers. If this hypothesis is upheld, then *Blepharicera* are differentially ingesting a high quality, easily digestible food resource (i.e., diatoms with adnate or prostrate growth forms). Alternatively, opposite trends of ingestibility and digestibility could exist in systems supporting a diversity of scrapers (e.g., Cataloochee Creek, where combinations of scraping Blephariceridae and Glossosomatidae exist year-round). According to Peterson *et al.* (1998), natural selection would favor digestion resistance in adnate and prostrate diatom cells (or taxa) in such systems. Although an interesting hypothesis, a study that quantifies the selective pressure exerted by guilds of scraping insects on diatom communities and considers counteractive factors such as rates of

downstream colonization of new (viable) cells and rates of diatom cell division is necessary to establish its validity.

Deviations in dietary assemblages from those of the forage base could reflect larval distribution on rocks relative to that of algal food resources, an unknown behavioral mechanism, or a morphological constraint. Although several descriptions of larval feeding in Blephariceridae exist [see Alverson *et al.* (2000) for synopsis], a detailed investigation of the mechanics of larval grazing might lend further insight to the mechanism by which larvae differentially ingest adnate and prostrate diatom species. One possibility is that larvae slowly [~2mm min^{-1} (Dudley *et al.* 1990, Frutiger 1998)] move across substrata "bulldozing" away species with conspicuous growth forms (e.g., *S. rumpens* and *S. ulna*). In our study, these conspicuous species were consistently ingested less frequently than expected, perhaps because they were less common in the modified (i.e., "bulldozed") forage base than in algal assemblages that we sampled to estimate ambient community structure. Regardless, a carefully designed experiment that closely monitors larval grazing of algae from glass slides—accounting for gut clearance rates, pre- and postgrazed assemblage structure of the forage base, larval gut contents, and downstream drift—would undoubtedly enhance our understanding of *Blepharicera* grazing patterns and mechanisms of selective feeding by grazers in general.

Our findings suggest that fourth-instar *Blepharicera* exert maximum grazing pressure on ambient algal assemblages at midstage as evidenced by increased total diatom cell ingestion in the second month of fourth-instar stadia for both species. Without estimates of ambient algal cell densities, increases cannot be attributed to increased grazing intensity with certainty; however, that the pattern was observed in both *Blepharicera* species would suggest that increases reflect changes in larval grazing activity rather than increases in environmental cell density. Finer scale (e.g., weekly) sampling should show a more gradual increase than we detected with monthly samples. Similar fluctuations in feeding intensity have been recorded

for larval Lepidostomatidae (Trichoptera) (Anderson and Grafius 1975). Some evidence suggests that *Blepharicera* discontinue feeding and empty their guts before larva–larva molts and larva–pupa molts (A. J. Alverson, unpublished data). This pattern is reflected in the increased diatom consumption of *B. similans* from June to July followed by decreased diatom cell ingestion in August. Guts of fourth-instar *B. similans* from September, 1998, contained very few diatom cells (A. J. Alverson, unpublished data).

Data from our study show that fourth-instar dietary assemblages can show considerable temporal variation (e.g., *B. similans*, summer), or they can remain invariable over time (e.g., *B. magna*, winter). Dietary changes sometimes reflected changes in ambient algal assemblages. Given the abundance of literature documenting larval requirement of rich food resources for final instars (Otto 1971, Winterbourn 1971, Anderson and Cummins 1979, Hart and Resh 1980, Fuller and Desmond 1997), knowledge of variation in nutritional value of commonly ingested periphyton species would lend value and insight to data from this and similar studies. The diets of *Blepharicera* instars I–III have not been studied, so it is unknown whether *Blepharicera* exhibit a dietary shift from nutritionally poorer food resources to diatoms in later instars as has been documented for other groups. In the absence of keys for early instar (I–III) *Blepharicera*, temporal changes in *Blepharicera* diets throughout the entire larval life history periods could be performed at sites that support only one blepharicerid species. Our data show that dietary assemblage structure and total cell ingestion can vary significantly throughout the final instar stadium for *Blepharicera*. It remains unclear whether other macroinvertebrate grazers exhibit temporal grazing trends similar to those of *Blepharicera*, and exactly what the implications of such functional variability are for benthic community structure and function.

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3.1. (a) CA ordination of winter *B. magna* gut samples (triangles) and ambient algal samples (circles) from Cataloochee Creek, North Carolina. Eigen values: Axis I = 0.315; Axis II = 0.133. (b) Ordination of selected diatom species (i.e., species that comprised an average of ≥6% of the total cells counted of at least one larval group or source sample). The nested box delimits the position of the sample ordination. See Table 3.2 for diatom species abbreviations.

Species scores
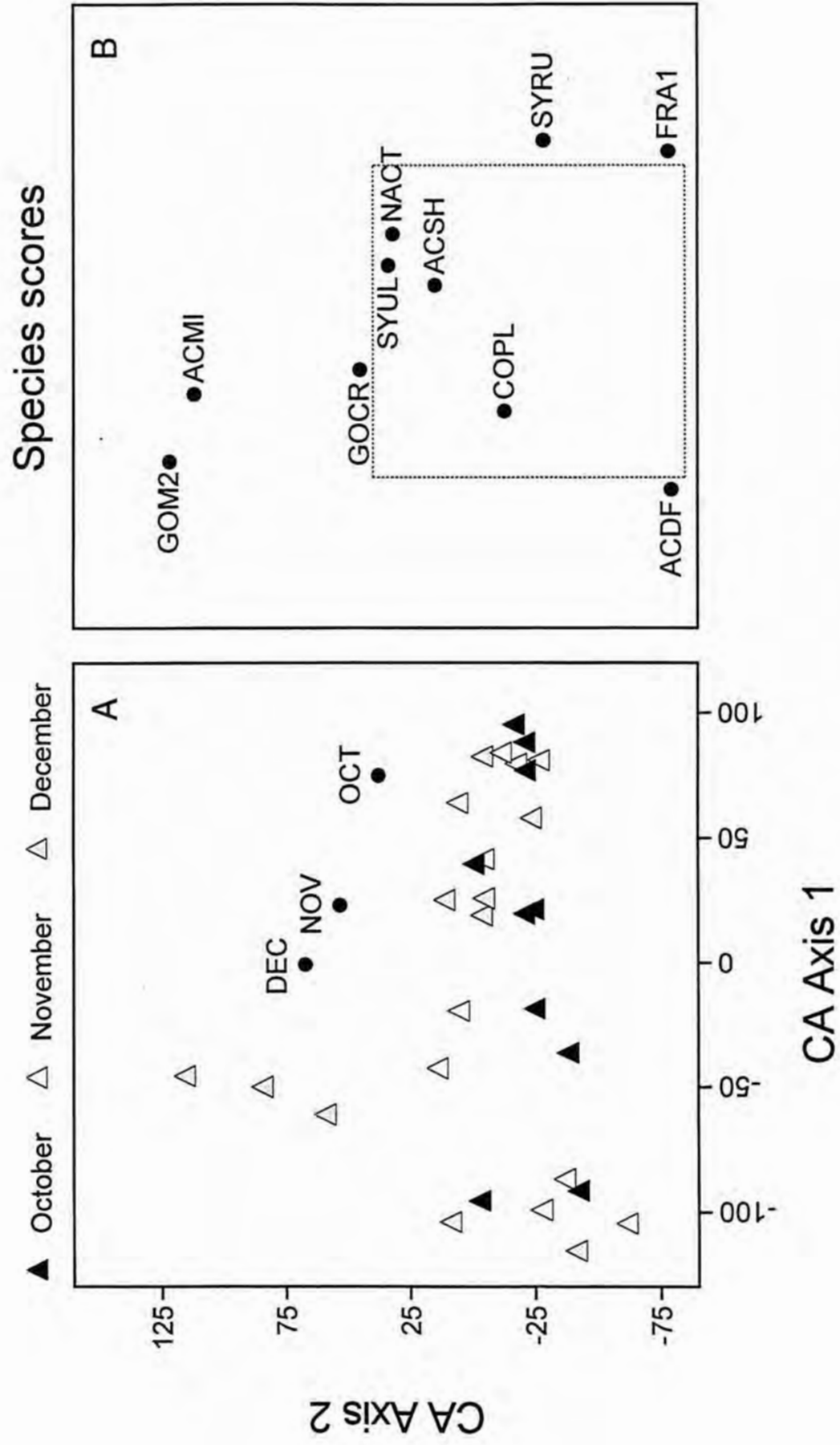
3.2. (a) Mean Bray-Curtis similarity (± 1 SE) between *B. magna* gut samples and the corresponding algal source sample in winter, 1998. Within a graph, columns with similar labels do not differ significantly ($p > 0.05$). (b) Mean number of diatom cells (± 1 SE) ingested per *B. magna* larva in winter, 1998. Within a graph, columns with similar labels do not differ significantly ($p > 0.05$).
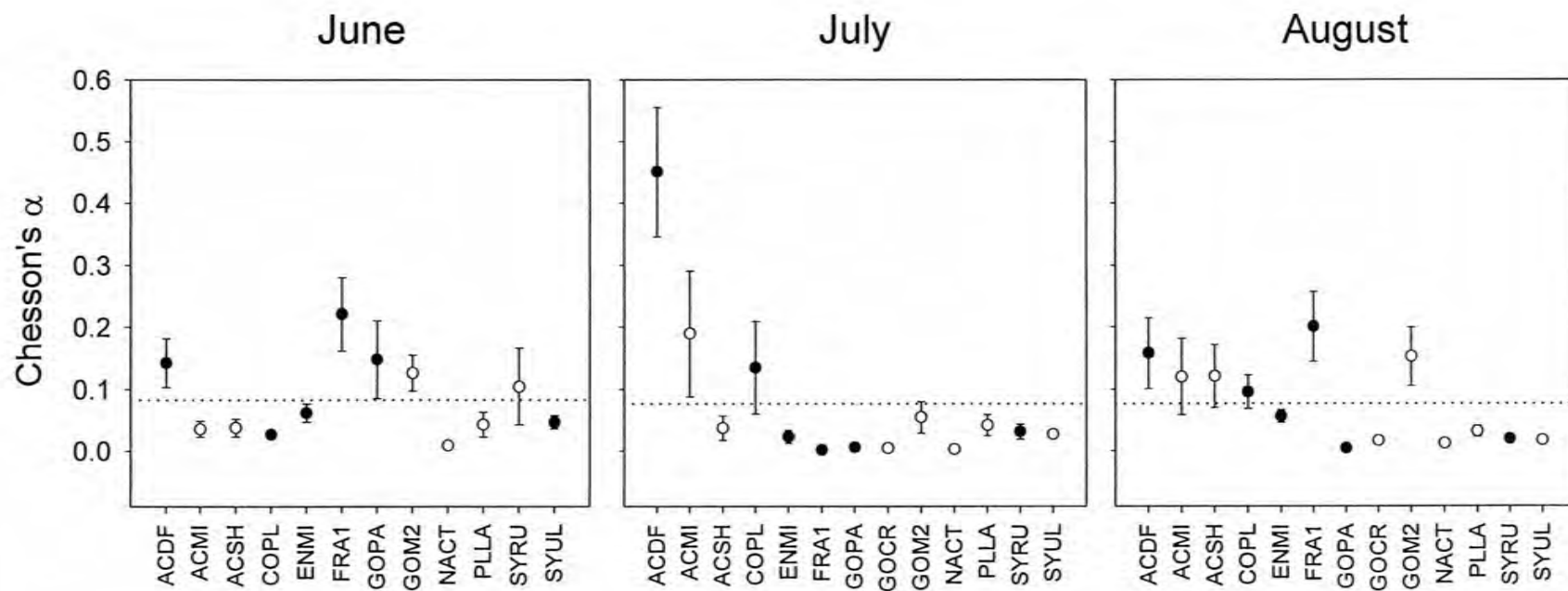
Blepharicera magna
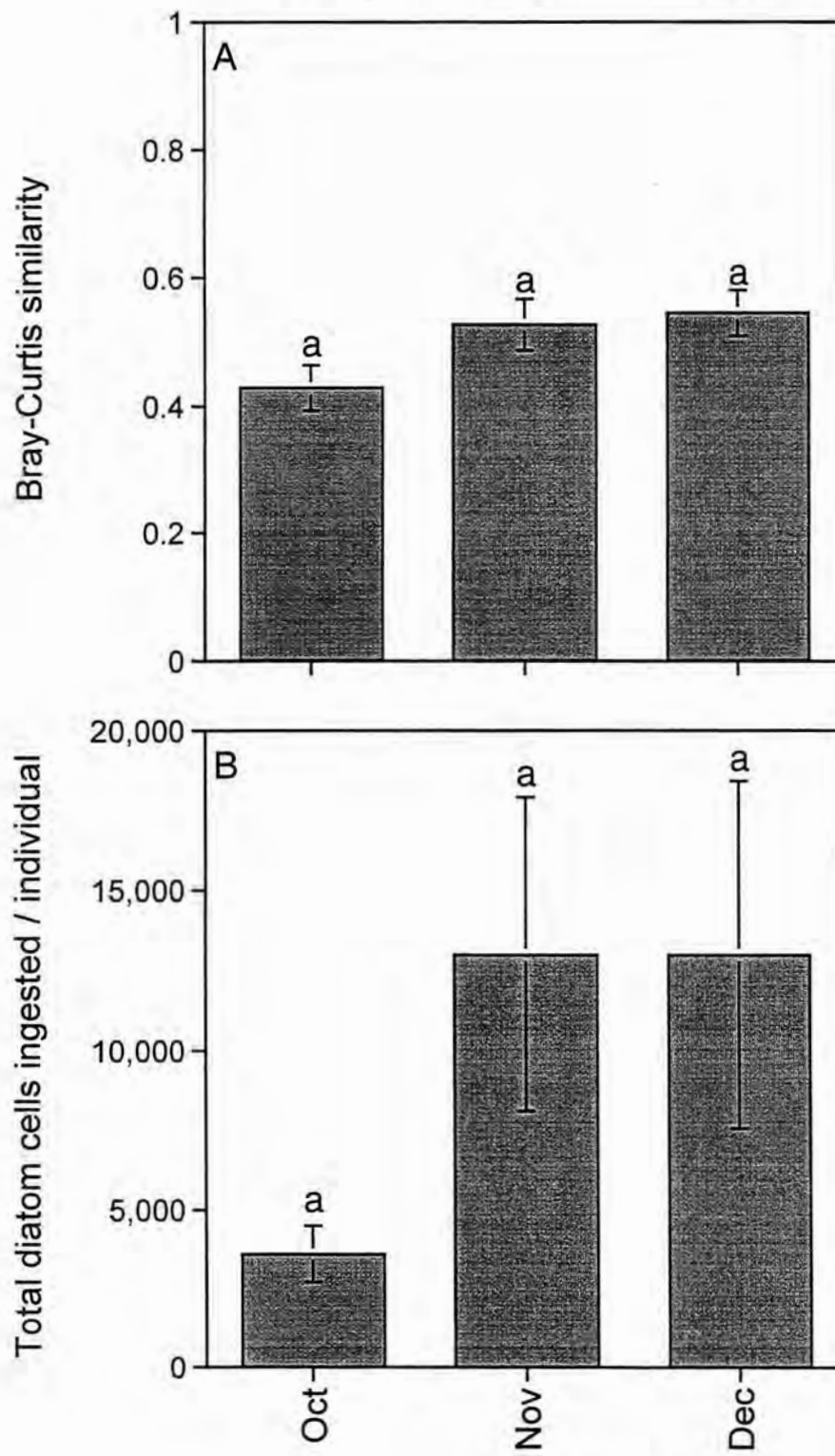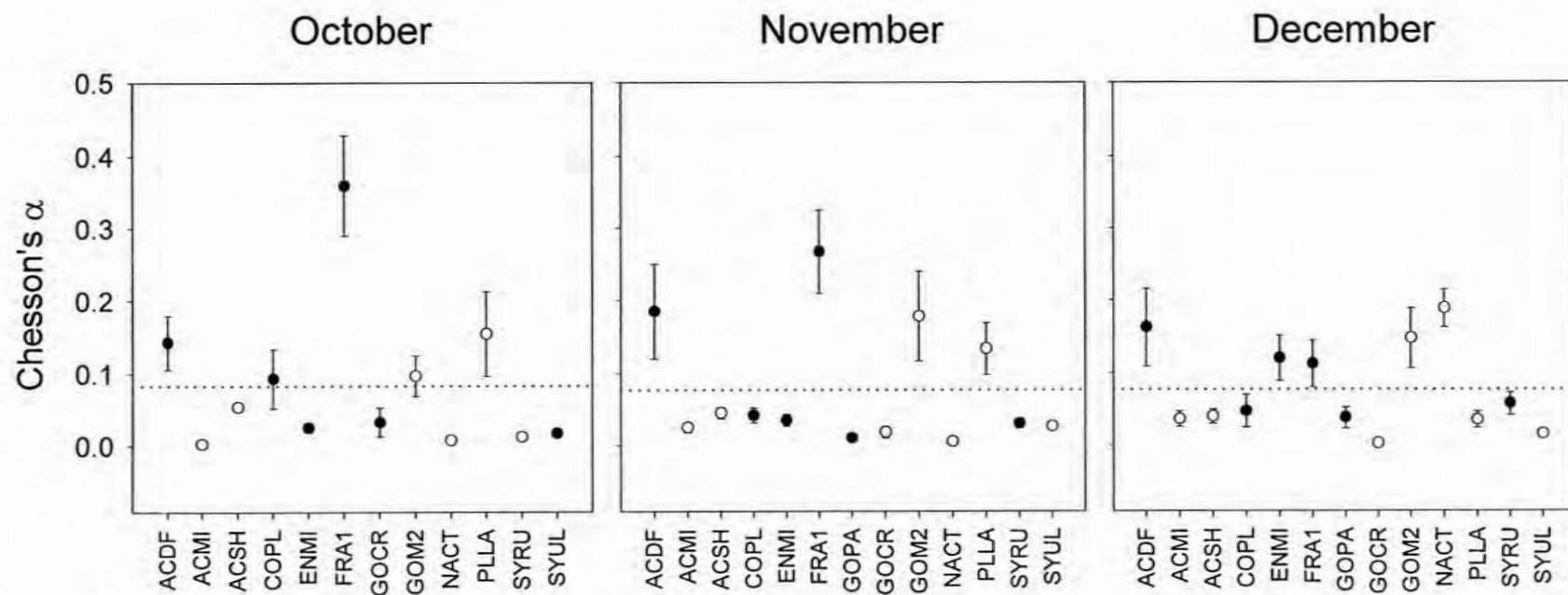
Fig. 3.3. Mean (±1 SE) Chesson's α values for the most commonly ingested diatom species by *B. magna* in winter, 1998. Dotted lines indicate expected values (October, 1/12=0.083; November and December, 1/13 = 0.077) for algal taxa if they occurred in the same proportion in larval guts as they did on the substratum. Filled circles indicate species that differed from zero, and open circles indicate species that did not (after sequential Bonferroni correction). See Table 3.2 for diatom species abbreviations.

3.4. (a) CA ordination of summer *B. similans* gut samples (diamonds) and ambient algal samples (circles) from Cataloochee Creek, North Carolina. Eigen values: Axis I = 0.392; Axis II = 0.314. (b) Ordination of selected diatom species (i.e., species that comprised an average of ≥6% of the total cells counted of at least one larval group or source sample). The nested box delimits the position of the sample ordination. See Table 3.2 for diatom species abbreviations.
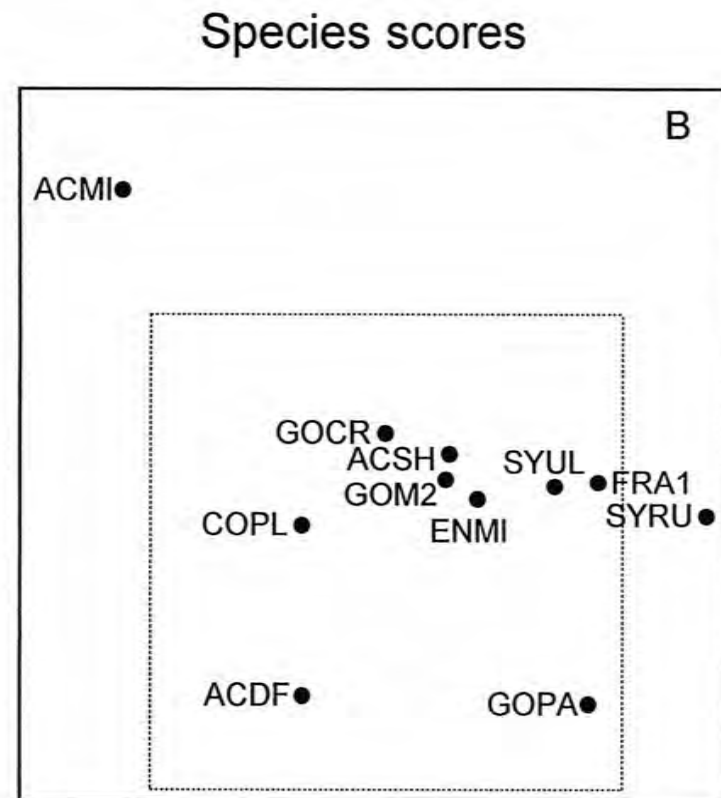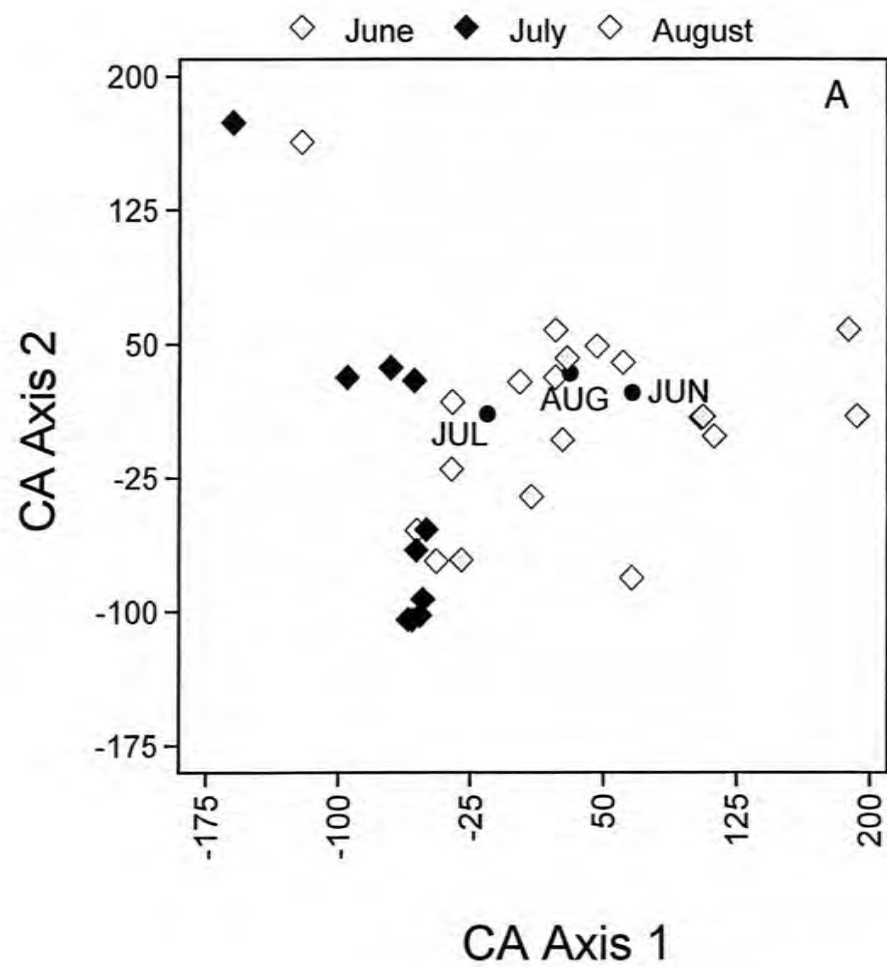
3.5. Mean Bray-Curtis similarity (±1 SE) between *B. similans* gut samples and the corresponding algal source sample in summer, 1999. Within a graph, columns with similar labels do not differ significantly (p > 0.05). 3.3B. Mean number of diatom cells (±1 SE) ingested per *B. similans* larva in summer, 1999. Within a graph, columns with similar labels do not differ significantly (p > 0.05).

Blepharicera similans
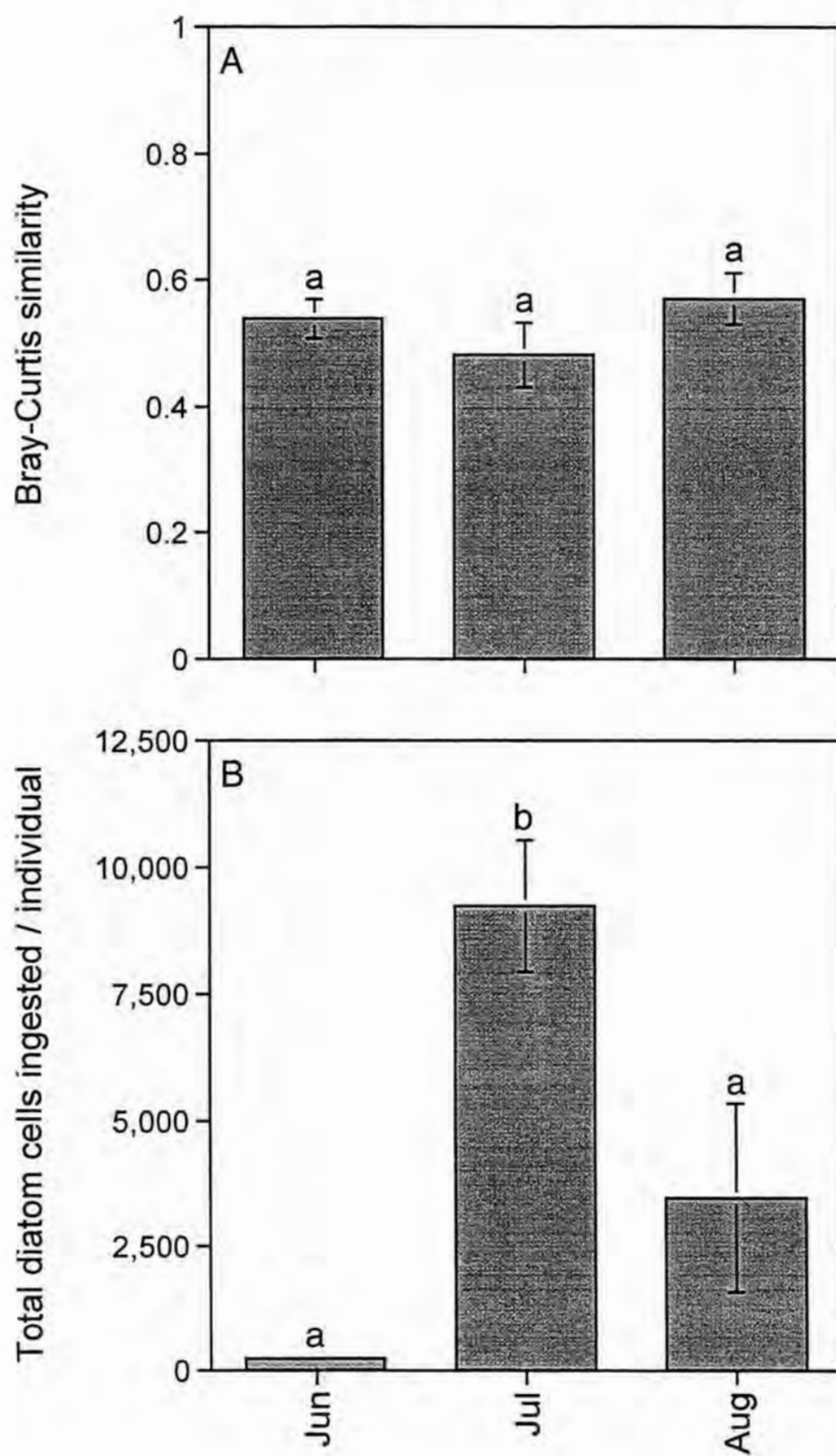
Fig. 3.6. Mean (±1 SE) Chesson's α values for the most commonly ingested diatom species by *B. similans* in summer, 1999. Dotted lines indicate expected values (June, 1/12=0.083; July and August, 1/13 = 0.077) for algal taxa if they occurred in the same proportion in larval guts as they did on the substratum. Filled circles indicate species that differed from zero, and open circles indicate species that did not (after sequential Bonferroni correction). See Table 3.2 for diatom species abbreviations.

Table 3.1. *Blepharicera* diversity and life history patterns at Cataloochee Creek, North Carolina. Life history classifications are *sensu* Johns (1996) and Courtney (2000). See text for details.

Species	Relative abundance	Life cycle type
B. magna Courtney	common	winter (Sep–Apr)
B. williamsae Alexander	common	winter (Dec–Mar)
B. coweetae Hogue and Georgian	common	winter (Dec–Mar)
B. appalachiae Hogue and Georgian	common	spring
B. cherokea Hogue	common	spring
B. tuberosa Courtney	common	spring
B. separata Alexander	rare	early summer
B. similans Johannsen	common	summer

Data based on collections from 1990 to 1999

Table 3.2. Average relative abundance and growth habits of the 16 most common diatom species from *Blepharicera* diets and ambient algal assemblages at Cataloochee Creek, North Carolina. Species codes identify taxa in figures.

Species	Species code	Growth habit	Relative abundance					
			B. magna / ambient			*B. similans* / ambient		
			Oct.	Nov.	Dec.	Jun.	Jul.	Aug.
Meridion circulare (Grev.) Ag.	MERI	circular filament-forming	0.0/0.0	0.2/0.1	0.1/0.0	3.2/0.9	0.0/0.7	0.0/0.4
Synedra rumpens (Kütz.)	SYRU	rosette-forming	14.1/53.3	10.2/22.0	10.7/11.4	12.5/12.1	0.6/4.0	2.6/7.5
Synedra ulna (Nitz.) Ehr	SYUL	rosette-forming	3.7/9.3	4.0/10.2	3.7/16.3	5.8/9.9	0.5/3.8	3.9/12.4
Fragilaria vaucheriae (Kütz.) Peters.	FRVA	chain-forming	1.8/3.2	2.8/3.5	3.8/3.5	3.2/3.8	0.0/1.0	1.1/2.0
Fragilaria vaucheriae v. #1	FRA1	chain-forming	3.6/28.5	26.9/6.8	15.9/9.0	7.0/2.4	0.0/2.2	3.8/1.0
Cocconeis placentula v. *lineata* (Ehr.) V.H.	COPL	adnate	10.2/5.7	8.9/14.8	7.6/12.4	4.2/12.9	23.4/39.3	19.0/16.7
Achnanthes deflexa v. *alpestris* Lowe & Kociolek	ACDF	adnate	31.0/8.7	33.9/13.4	33.3/16.7	32.3/20.4	61.5/27.8	34.1/22.0
Achnanthes subhudsonis v. *kraeusellii* Choln.	ACSH	adnate	6.3/5.1	6.4/9.2	7.8/12.0	2.1/3.8	0.3/1.3	7.5/4.1
Planothidium lanceolatum (Bréb) Round & Bukhtiyarova	PLLA	adnate	0.4/0.1	0.2/0.1	0.2/0.4	2.8/4.9	0.6/2.3	0.8/1.4

Table 3.2. (continued)

Species	Species code	Growth habit	Relative abundance					
			B. magna / ambient			B. similans / ambient		
			Oct.	Nov.	Dec.	Jun.	Jul.	Aug.
Achnanthidium minutissimum (Kütz.) Czarnecki	ACMI	adnate	0.1/1.3	1.9/4.5	4.0/6.6	1.8/4.1	10.7/5.1	9.7/4.7
Achnanthes sp. #1	ACH1	adnate?	0.3/2.3	0.3/0.8	1.0/0.1	0.0/0.0	0.0/0.4	0.0/0.0
Navicula cryptotenella Lange-Bertalot	NACT	motile	0.3/1.6	0.6/8.0	1.4/0.4	0.6/4.5	0.0/2.2	0.6/2.8
Encyonema minutum (Hilse in Rabenhorst) Mann	ENSI	mucilagenous tube-/mat–forming	0.4/0.8	0.7/1.4	1.5/0.7	4.8/6.3	0.4/3.0	5.3/5.9
Gomphonema parvulum (Kütz.) Kütz.	GOPA	pedunculate	0.0/0.3	0.2/1.1	0.4/0.7	7.7/3.6	0.0/1.2	0.0/0.3
Gomphonema christenseni Lowe & Kociolek	GOCR	pedunculate?	0.3/0.5	0.1/0.5	0.1/4.5	0.0/0.8	0.0/0.6	2.7/10.8
Gomphonema sp. #2	GOM2	pedunculate?	1.0/0.5	1.6/0.5	7.6/3.2	6.8/3.8	0.7/1.9	7.3/2.8

Table 3.3. Results of Mantel permutation tests testing the null hypothesis of no difference in dietary assemblages of different larval groups.

| | B. magna | | | B. similans | |
	October	November	December	June	July
November	r = -0.03 p = 0.38	—			
December	r = 0.06 p = 0.14	r = 0.02 p = 0.27	—		
June	r = 0.31 p < 0.01	r = 0.23 p = 0.01	r = 0.13 p = 0.04	—	
July	r = 0.46 p < 0.001	r = 0.37 p < 0.001	r = 0.37 p < 0.001	r = 0.40 p < 0.001	—
August	r = 0.40 p < 0.001	r = 0.28 p < 0.01	r = 0.18 p = 0.02	r = 0.21 p < 0.01	r = 0.21 p < 0.01

Bonferroni-corrected type 1 error rate is $\alpha = 0.003$

CHAPTER 4. GENERAL CONCLUSIONS

Ecologically speaking, Blephariceridae have been and still are a poorly known group. With few exceptions, previous descriptions of blepharicerid ecology have been anecdotal; in fact, most accounts have been supplementary to taxonomic descriptions and systematic investigations—studies that establish the foundation from which ecologists build. The objective of this investigation was to establish a baseline description of larval feeding characteristics for Appalachian *Blepharicera*. The question was a simple one, though estimable because it had yet to be formally addressed. The impetus for this research was the perplexingly high degree of spatiotemporal overlap of congeneric *Blepharicera* in southern Appalachian streams. Gause's competitive exclusion principle prohibits such marked sympatry in the absence of some mechanism of ecological segregation (e.g., differential utilization of food resources). That we might show ecological segregation of congeners through partitioning of food resources was the prize that stood to be potentially manifest through a simple dietary study like this one.

I have provided a rigorous, qualitative and quantitative description of blepharicerid dietary characteristics as they relate to generalized patterns of larval distribution within streams, coexistence of congeneric species, and temporal changes in larval diets. In doing so, some poorly understood aspects of blepharicerid life history and ecology are now clarified.

Larval *Blepharicera* from the southern Appalachian Mountains are rheophilic specialists, and they constitute a guild of highly specialized, true scrapers that feed almost exclusively on epilithic diatoms. Larval mouthparts enable *Blepharicera* to harvest understory diatom species with adnate and prostrate growth forms. Given the available literature, this attribute is somewhat unusual among most groups of lotic macroinvertebrate grazers. The high degree of local sympatry in the *Blepharicera* fauna in southern Appalachian streams is enigmatic in light of the rich regional diversity, restrictive ecological requirements of *Blepharicera*, and homogeneity of mouthpart structure among congeners. Within a generalized

microhabitat where spatial overlap of larval *Blepharicera* was most acute, only weak evidence was found in support of the hypothesis that congeners coexist through partitioning of the food resources. Data often showed large, significant differences in the dietary assemblages of larvae occupying different microhabitats, suggesting that mechanisms of temporal and spatial isolation of sympatric *Blepharicera* might sufficiently minimize interspecific competition for food. Data also showed significant differences in total diatom cell ingestion among conspecifics that inhabit riffles with different free-stream current velocities. Future investigations should consider ambient algal cell densities and incorporate reciprocal transplant manipulations to determine the complex interaction of larval grazing with current velocity and availability of algal food resources.

Examination of temporal changes in diatom ingestion by *B. magna* and *B. similans* showed that larval diets can vary both quantitatively and qualitatively throughout the fourth-instar stadium. Qualitative differences in diatom ingestion sometimes did and sometimes did not reflect changes in ambient algal assemblages. Future investigations into the nutritional value of commonly ingested diatom species might show that observed grazing patterns reflect larval preference for higher quality food resources at some critical growth period in the fourth-instar stage. Data also showed that larvae exert maximum grazing pressure during midstage, and that total diatom consumption can decline near the end of the fourth-instar stadium. Although this observation is a likely reflection of intensified larval grazing, fluctuations could result from increases in environmental diatom cell density. Evaluation of larval grazing efficiency again revealed that *Blepharicera* are particularly good at ingesting small, adnate diatom species.

In total, this investigation considered the dietary characteristics of 8 insect species, more species than any other investigation of its kind. In addition, data were analyzed using a variety of traditional and nontraditional techniques, many of which are not presented in this thesis. Several of the analyses were ultimately included to remind freshwater benthic

ecologists of their existence, who despite their brilliance, have become remarkably predictable and often irresponsible in their choice of statistical analyses. This work, though by no means monumental, represents a small contribution to our understanding and appreciation of blepharicerid life history and ecology.

ACKNOWLEDGEMENTS

I would like to thank Drs. Greg Courtney, John Downing, Elliot Krafsur, and Mark Luttenton for serving on my graduate committee and providing helpful advice and guidance throughout this study. I am especially grateful to Dr. Courtney for nurturing my scientific interests since I was a young undergraduate at Grand Valley State University; for affording me the opportunity to carry out this research; for allowing great freedom to perform this work as I saw appropriate; and for being a trusted friend and mentor. I thank/blame Dr. Mark Luttenton for sparking my interest in diatoms. Daily exchanges with Dr. Elliot Krafsur about all things entomological, biological, political, philosophical, personal and otherwise were cherished and will be greatly missed. David Coyle, Laura Hansen, Matthew Murphy, Michael Schiavone, and several others made my moment at Iowa State University a rich one. The encouragement and interest of Katey Alverson, Amy and Cal Hodgson, Andrew D. Krino, Jamie C. FitzGerald, Michael A. Setlock, and Todd M. Wilson were much appreciated and will not soon be forgotten—it's many a river that waters the land.

APPENDIX A. LIGHT MICROGRAPHS OF COMMON DIATOM SPECIES FROM *BLEPHARICERA* GUTS AND AMBIENT ALGAL ASSEMBLAGES

Figs. 1–2.   *Meridion circulare* (Grev.) Ag.

Figs. 3–5.   *Diatoma mesodon* (Ehr.) Kütz.

Fig. 6.   *Diatoma vulgaris* Bory

Figs. 7–8.   *Synedra rumpens* (Kütz.)

Fig. 9.   *Synedra ulna* (Nitz.) Ehr

Fig. 10.   *Synedra* sp. cf. *ulna*

Fig. 11.   *Fragilaria vaucheriae* (Kütz.) Peters.

Fig. 12.   *Fragilaria vaucheriae* v. #1
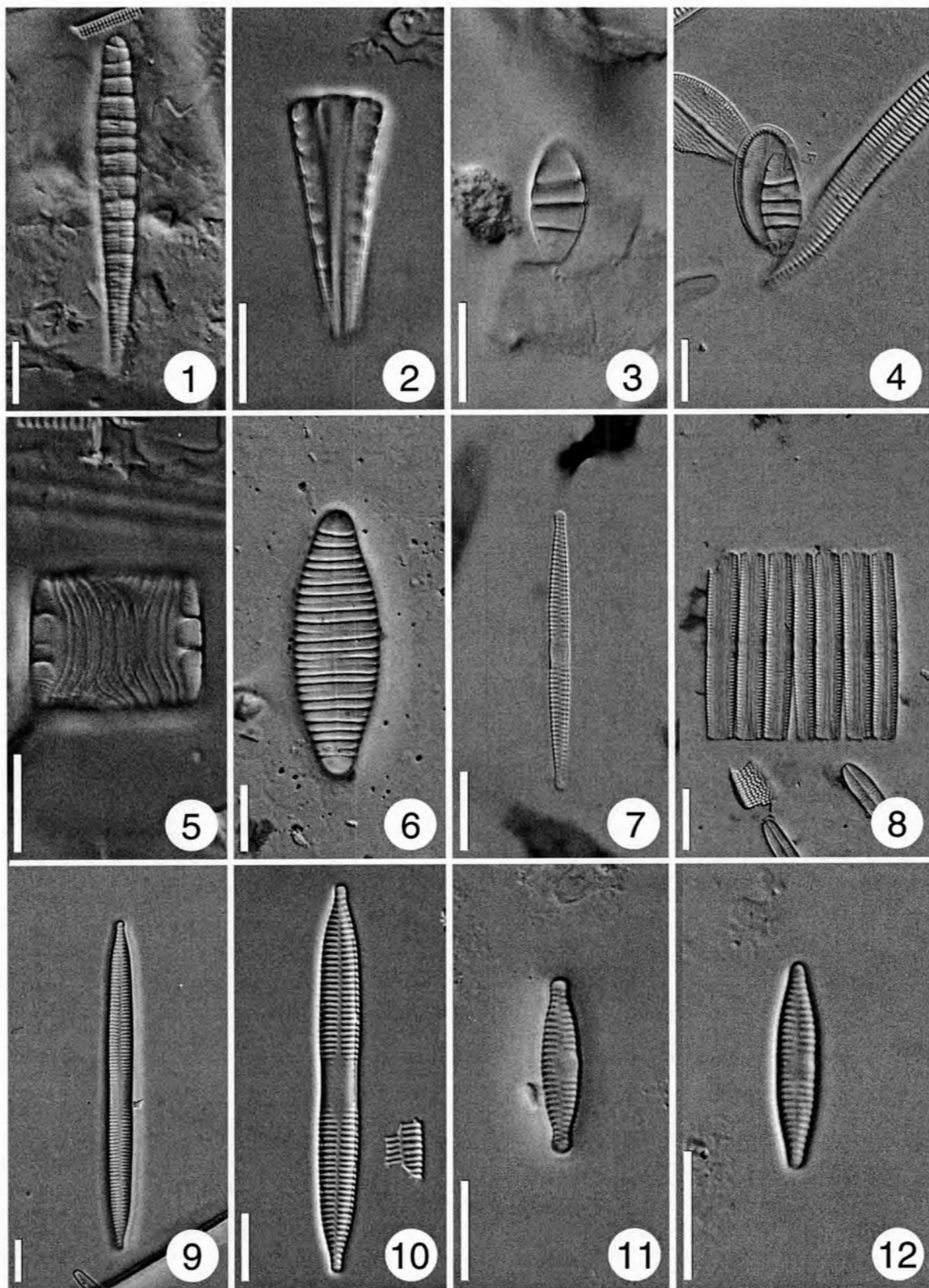
Figs. 13–14. *Cocconeis placentula* v. *lineata* (Ehr.) V.H.

Figs. 15–18. *Achnanthes deflexa* v. *alpestris* Lowe & Kociolek

Figs. 19–20. *Achnanthes subhudsonis* v. *kraeusellii* Choln.

Figs. 21–22. *Achnanthes* sp. #1

Figs. 23–24. *Achnanthes* sp. #5
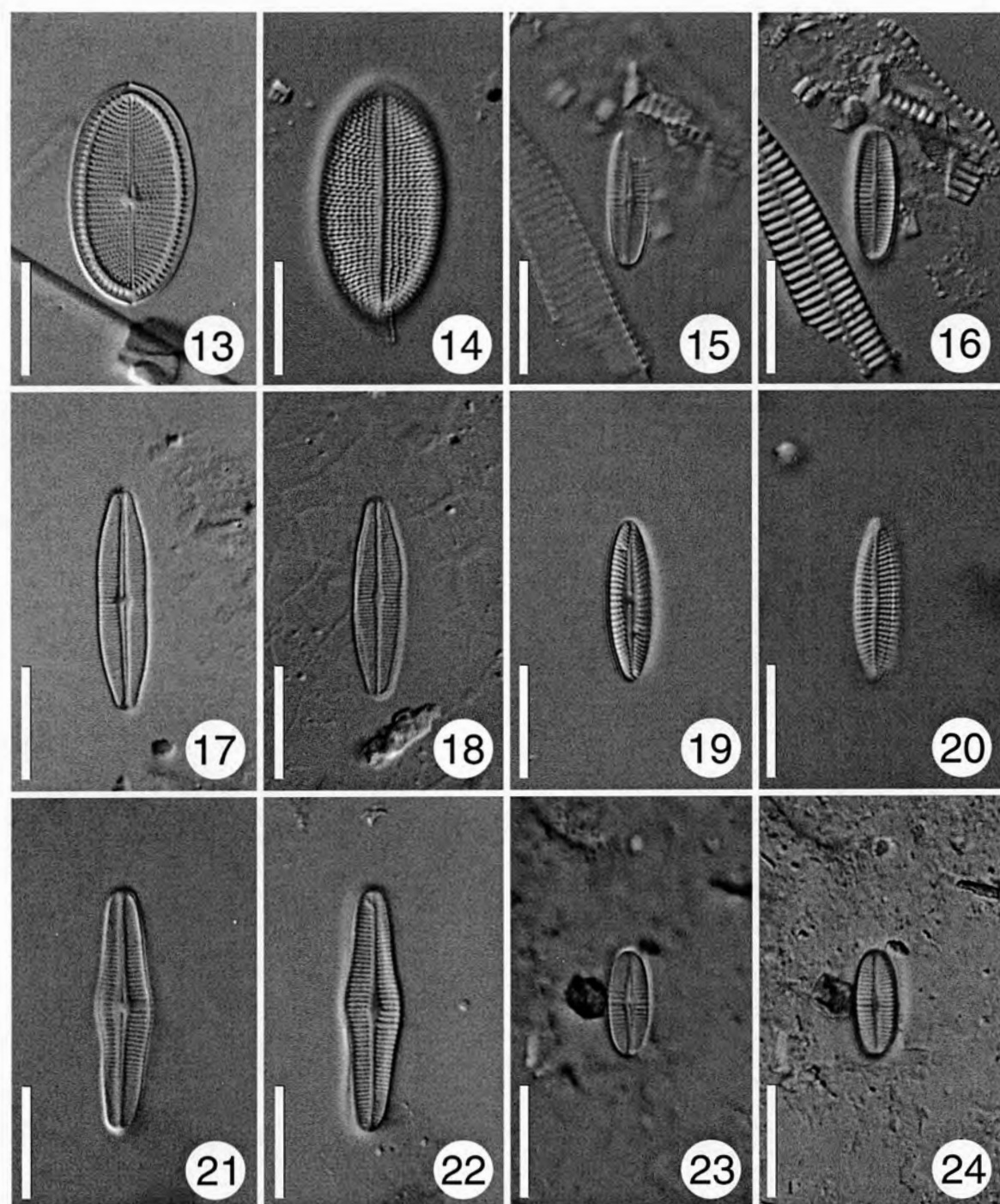
Figs. 25–26. *Planothidium lanceolatum* (Bréb) Round & Bukhtiyarova

Figs. 27–29. *Achnanthidium minutissimum* (Kütz.) Czarnecki

Figs. 30–32. *Eunotia* spp.

Fig. 33. *Navicula angusta* Grun.

Fig. 34. *Navicula cryptotenella* Lange-Bertalot

Fig. 35. *Navicula lanceolata* (Ag.) Kütz.

Fig. 36. *Navicula tripuncta* (O.F. Müll.) Bory
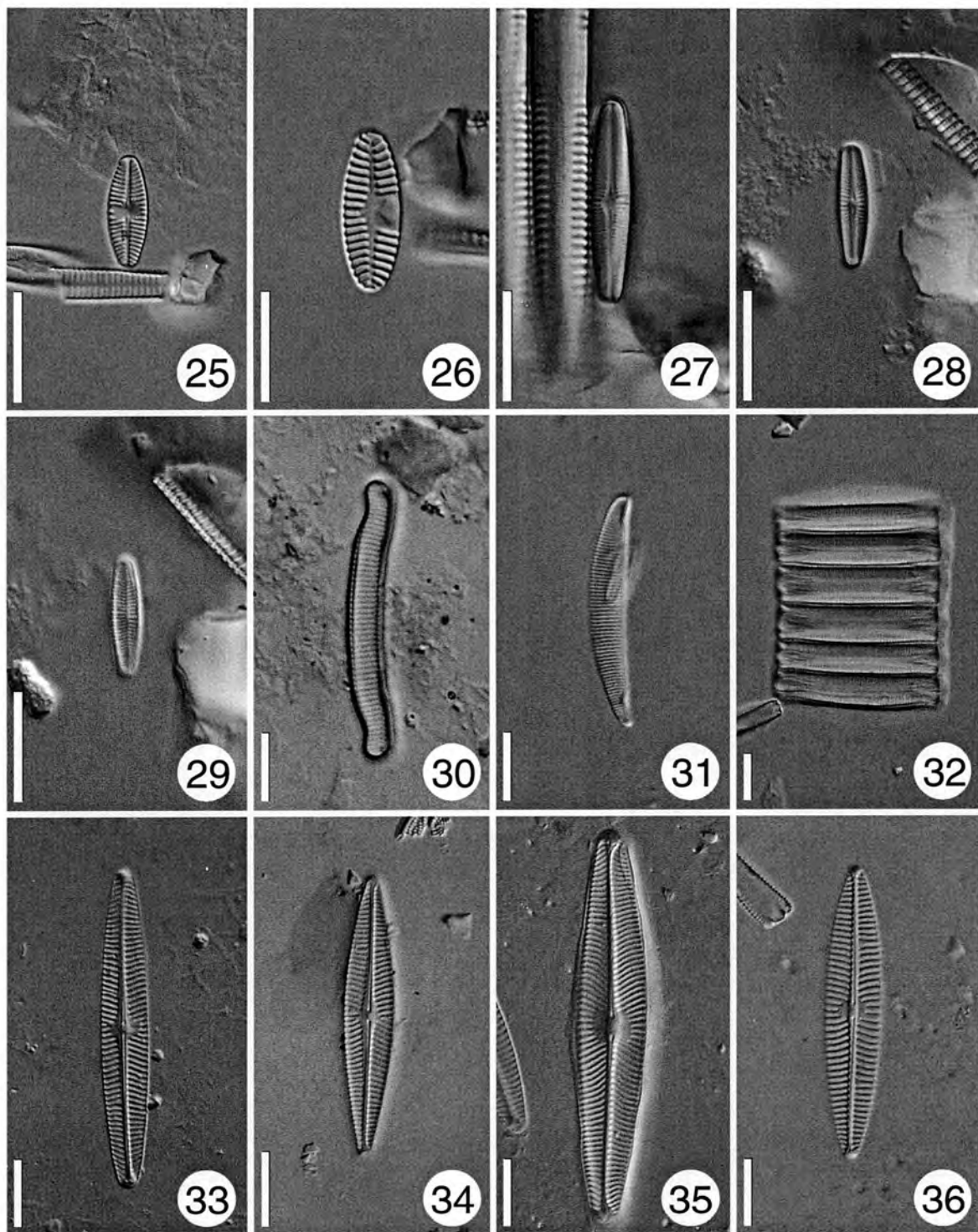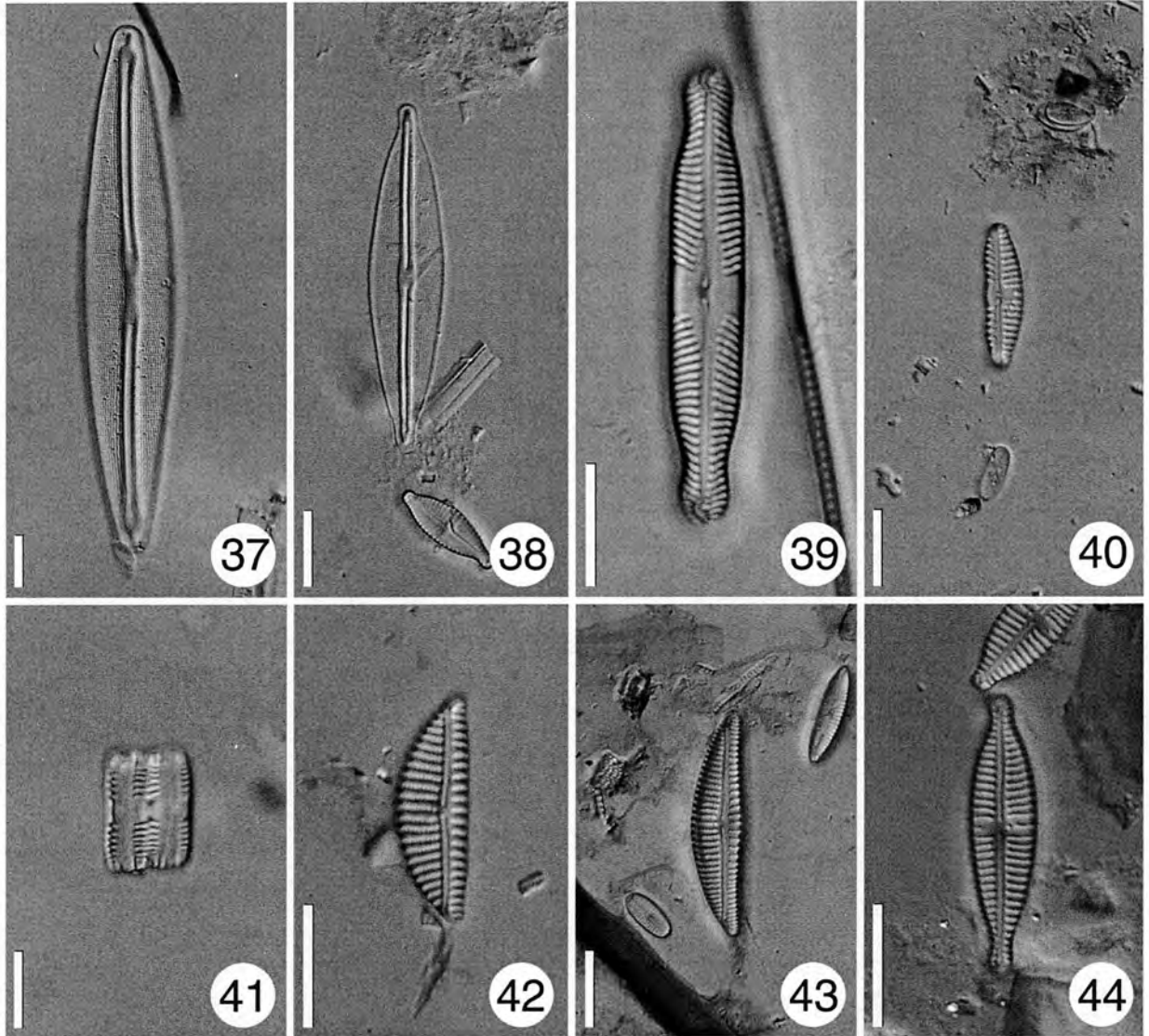
Fig. 45.   *Gomphonema christenseni* Lowe & Kociolek

Figs. 46–47.   *Gomphonema subclavatum* (Grun.) Grun.

Figs. 48–49.   *Gomphonema* sp. #1

Figs. 50–51.   *Gomphonema* sp. #2

Figs. 52–53.   *Gomphonema* sp. #5

Fig. 54.   *Nitzschia* spp.

Figs. 55–56.   *Epithemia adnata* (Kütz.) Bréb
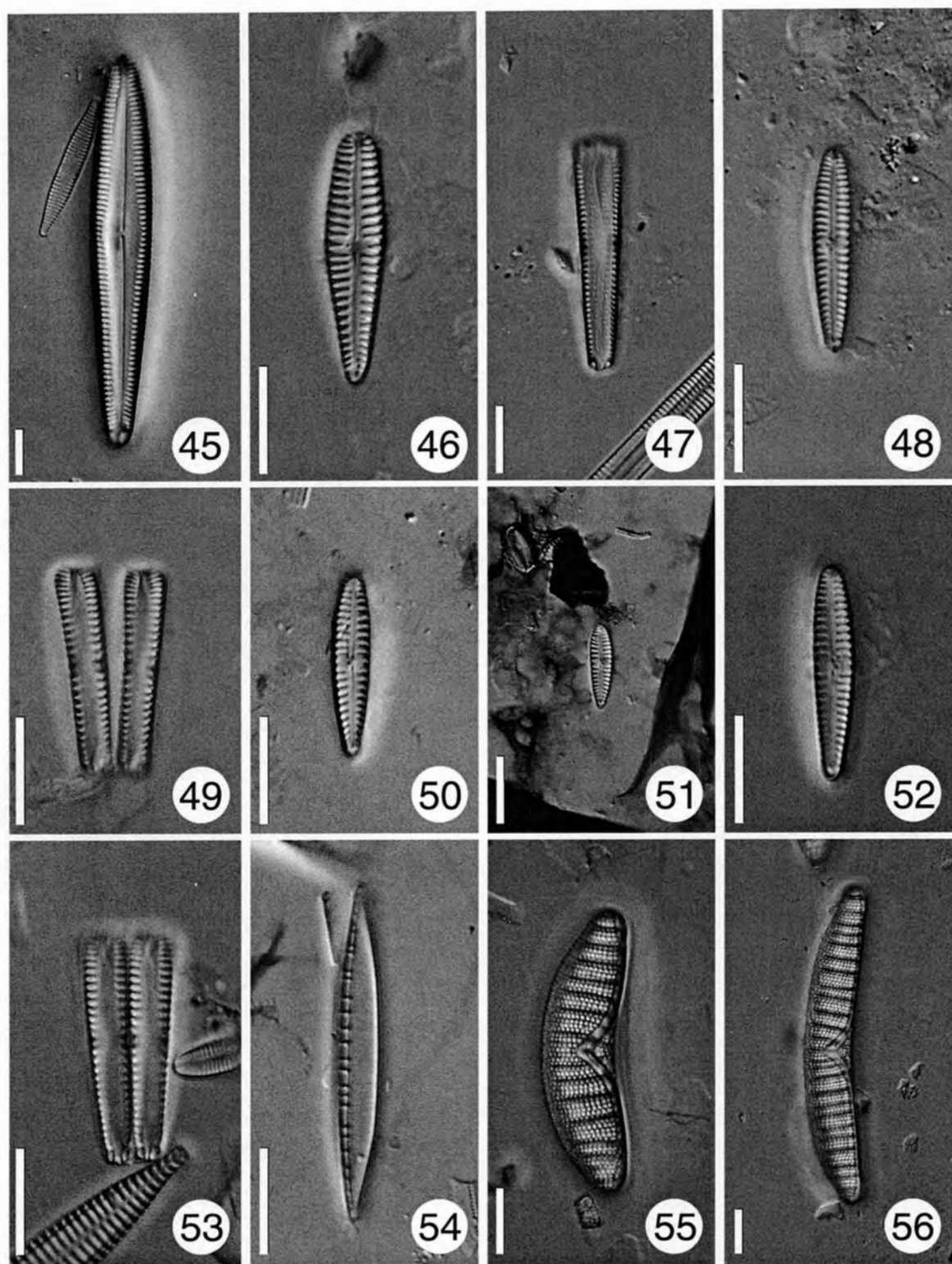
APPENDIX B. DIETARY DATA FOR APPALACHIAN *BLEPHARICERA*, SUPPLEMENTARY TO CHAPTER 2
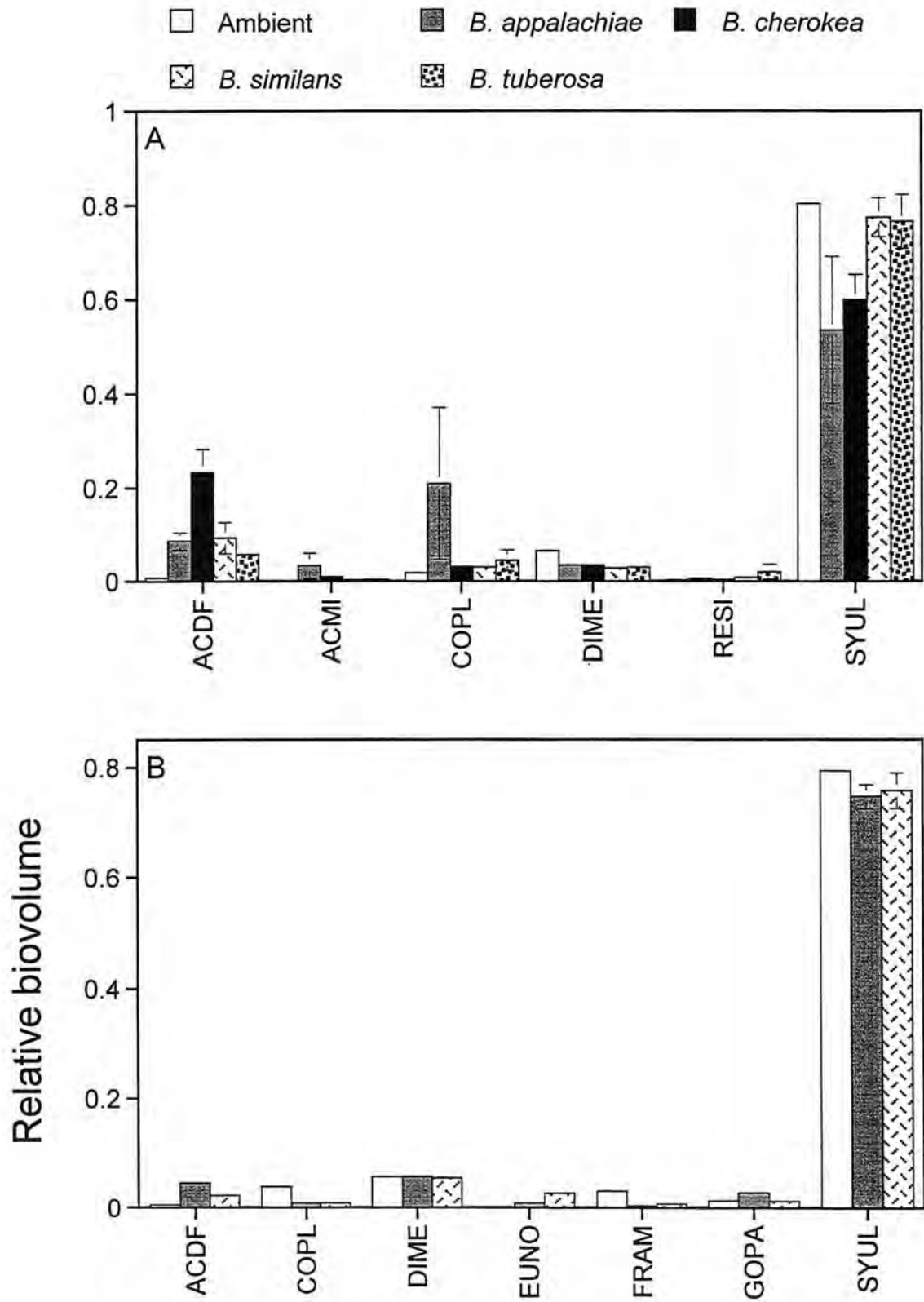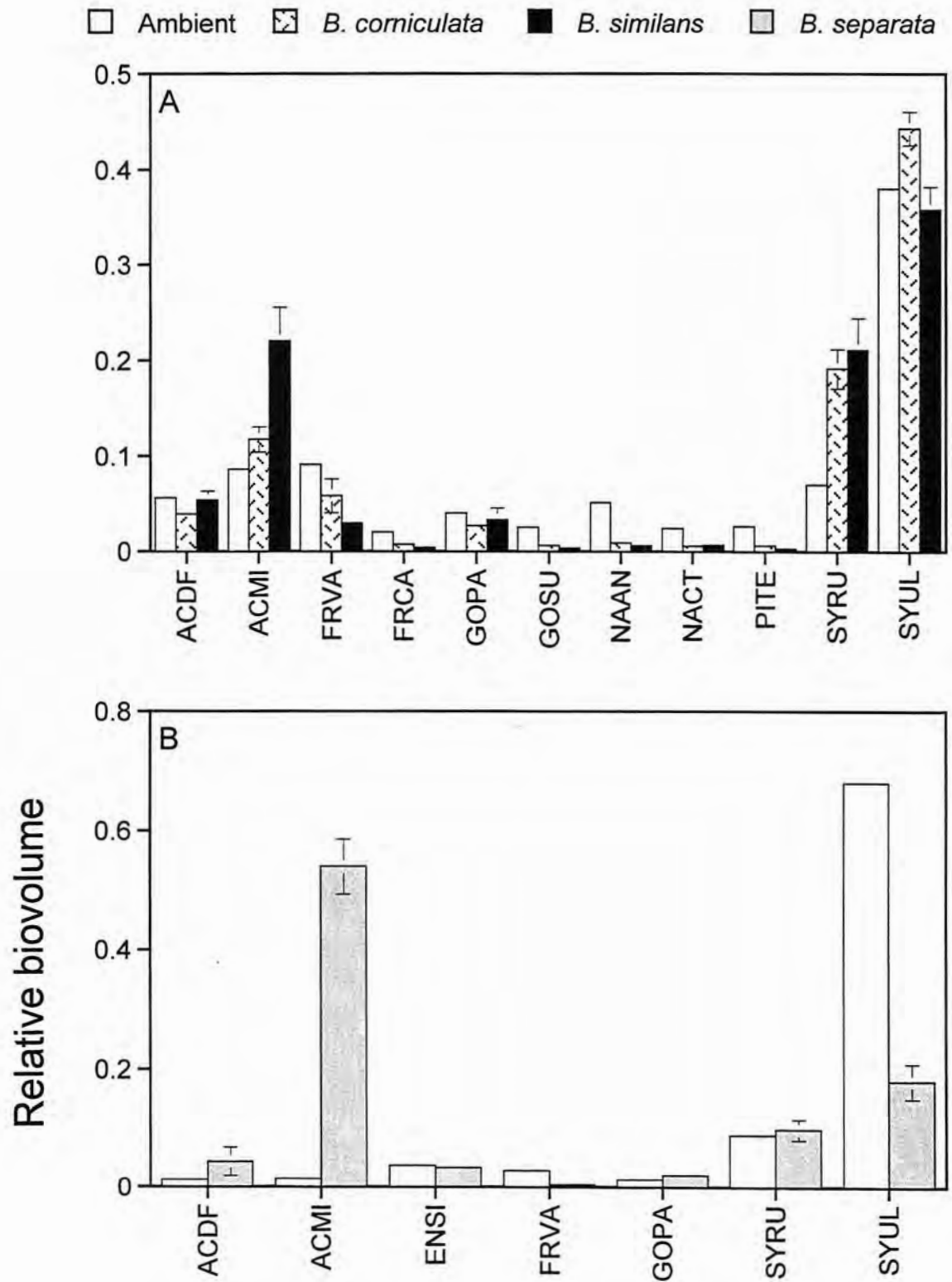
Fig. 1. Relative biovolume of major diatom taxa in gut contents of larval *Blepharicera* from Brasstown Falls, South Carolina. (a) Frequency histogram comparing relative biovolume of major diatom taxa in ambient algal assemblage and larval gut contents of *Blepharicera* from the base of Brasstown's lower falls (crash zone). (b) Frequency histogram comparing relative biovolume of major diatom taxa in ambient algal assemblage and larval gut contents of *Blepharicera* from a hygropetric zone. See Table 2.2 for diatom abbreviations.
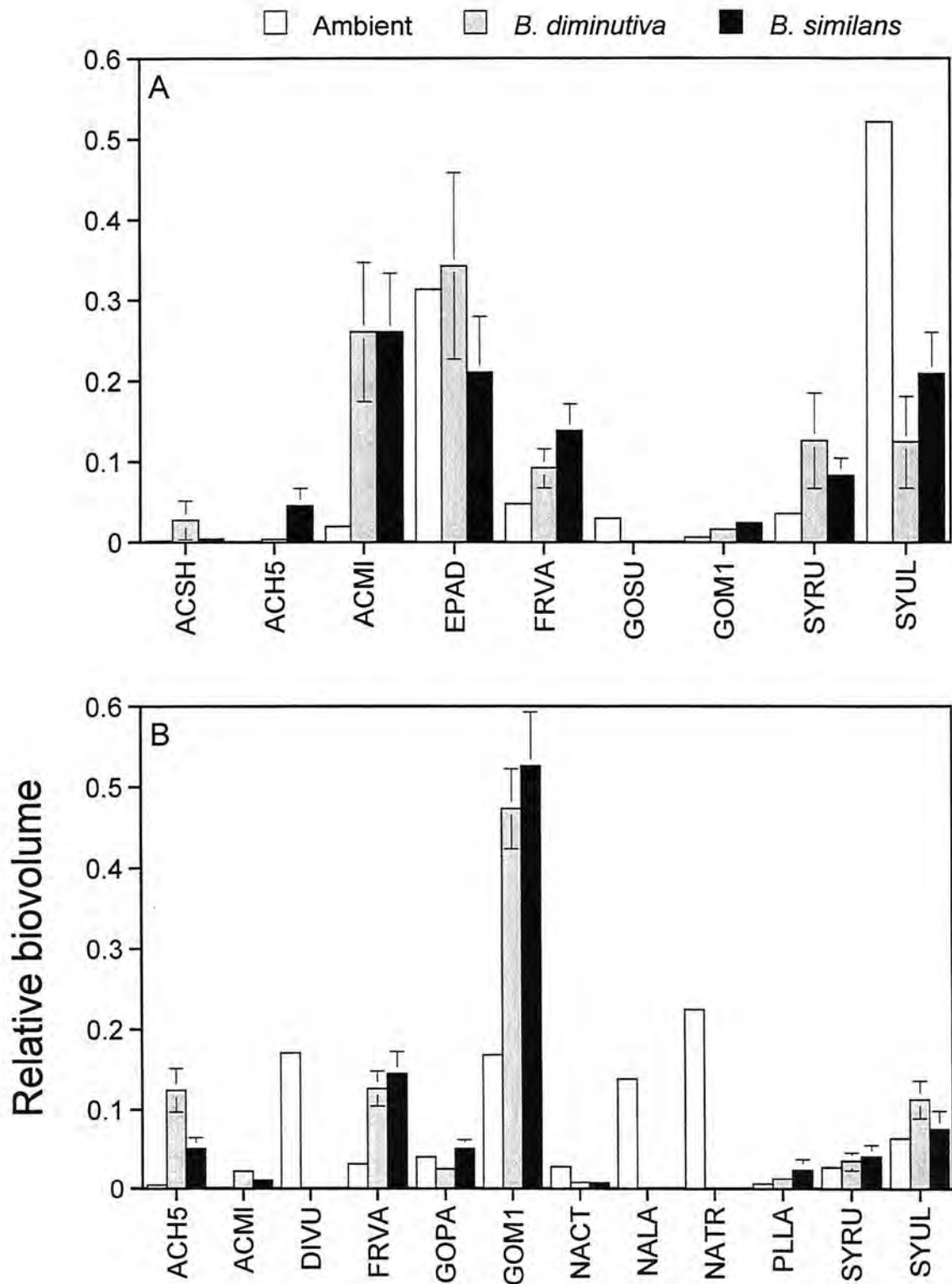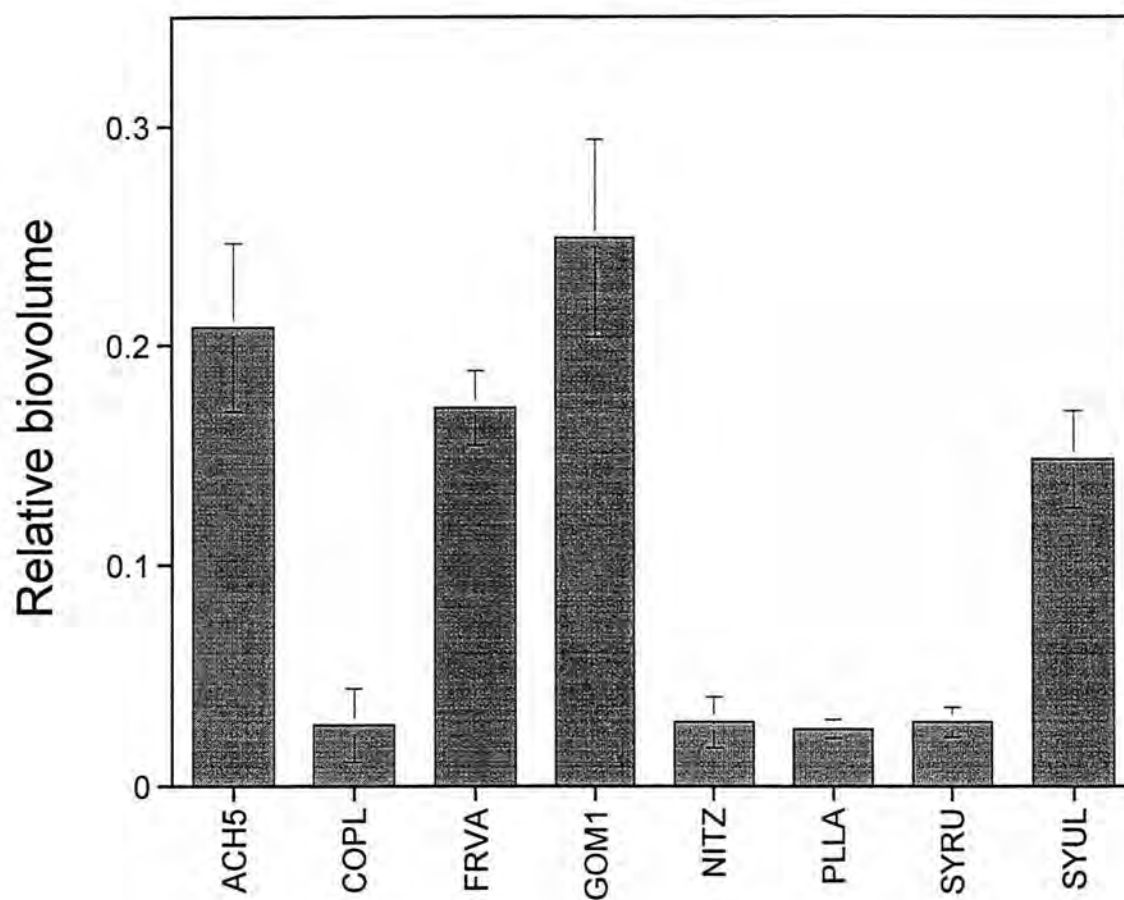
Fig. 2. Frequency histogram comparing relative biovolume of major diatom taxa in larval gut contents of *B. similans* from the cascade at Brasstown Falls, South Carolina. See Table 2.2 for diatom abbreviations.

Fig. 3. Relative biovolume of major diatom taxa in gut contents of larval *Blepharicera* from Cataloochee Creek, North Carolina. (a) Frequency histogram comparing relative biovolume of major diatom taxa in ambient algal assemblage and larval gut contents of *Blepharicera* from the fast riffle. (b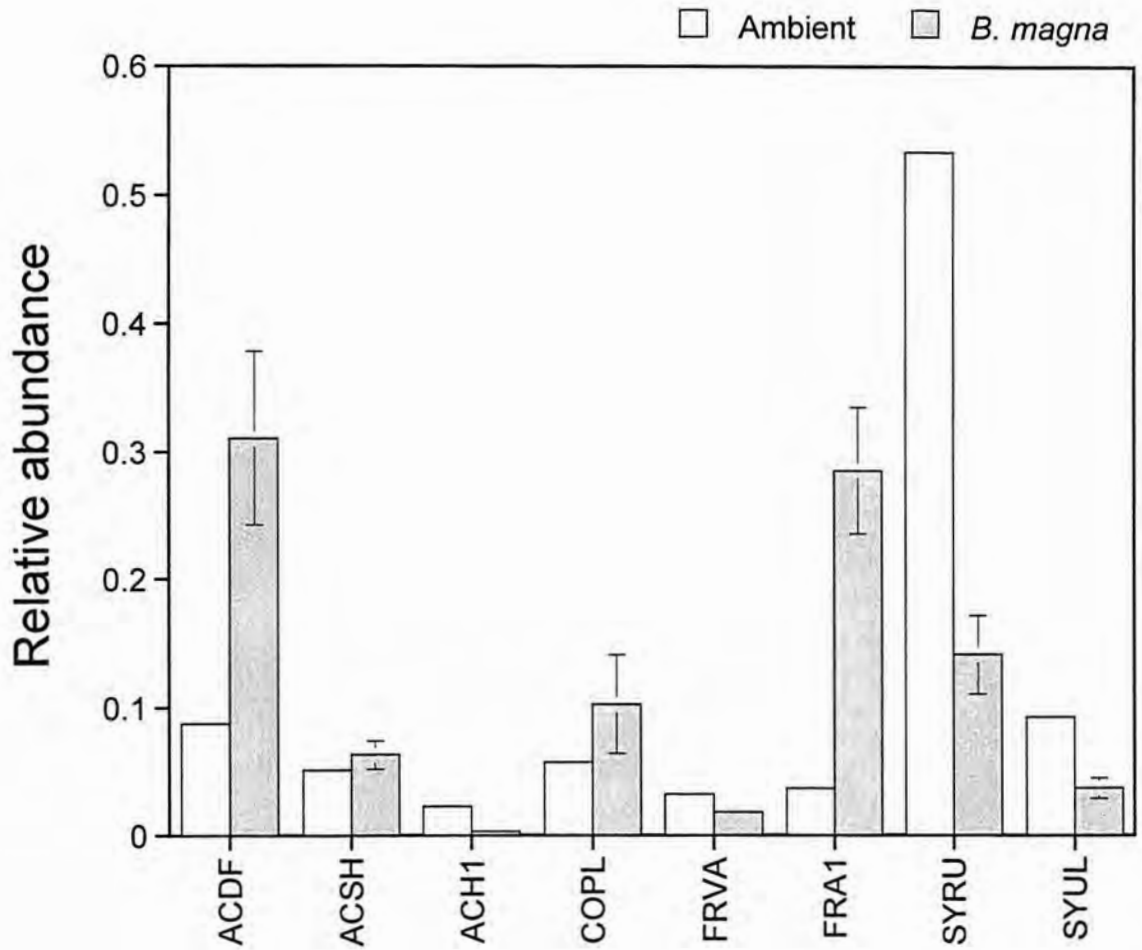) Frequency histogram comparing relative biovolume of major diatom taxa in ambient algal assemblage and larval gut contents of *Blepharicera* from slow riffle. See Table 2.2 for diatom abbreviations.

Fig. 4. Relative biovolume of major diatom taxa in gut contents of larval *Blepharicera* from Chattooga River, South Carolina. (a) Frequency histogram comparing relative biovolume of major diatom taxa in ambient algal assemblage and larval gut contents of *Blepharicera* from the chute. (b) Frequency histogram comparing relative biovolume of major diatom taxa in ambient algal assemblage and larval gut contents of *B. separata* from slow riffle. See Table 2.2 for diatom abbreviations.

APPENDIX C. DIETARY DATA FOR *B. MAGNA* AND *B. SIMILANS* FROM
CATALOOCHEE CREEK, NORTH CAROLINA, SUPPLEMENTARY TO CHAPTER 3

Fig. 1. Frequency histogram comparing relative abundance of major diatom taxa in ambient algal assemblage and larval gut contents of *B. magna* from Cataloochee Creek, North Carolina, in October, 1998. See Table 3.2 for diatom abbreviations.
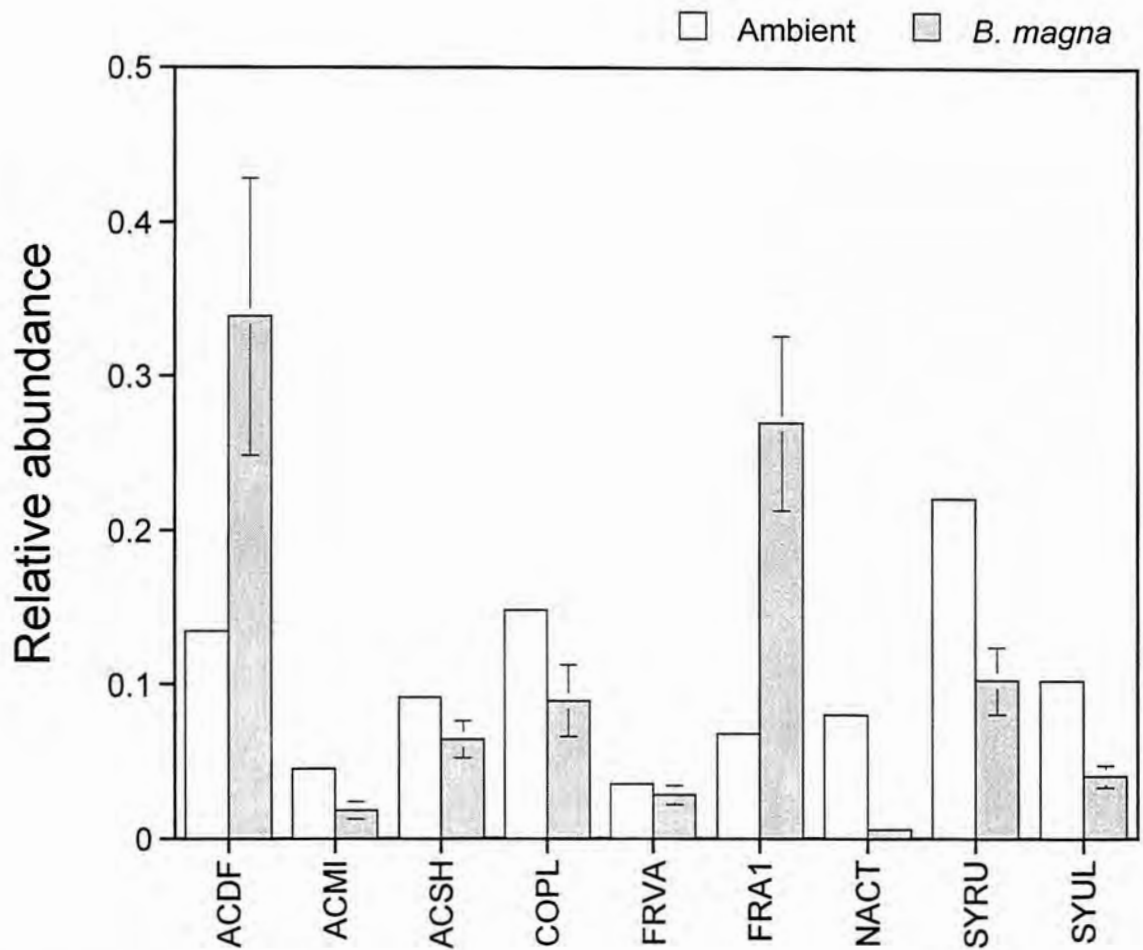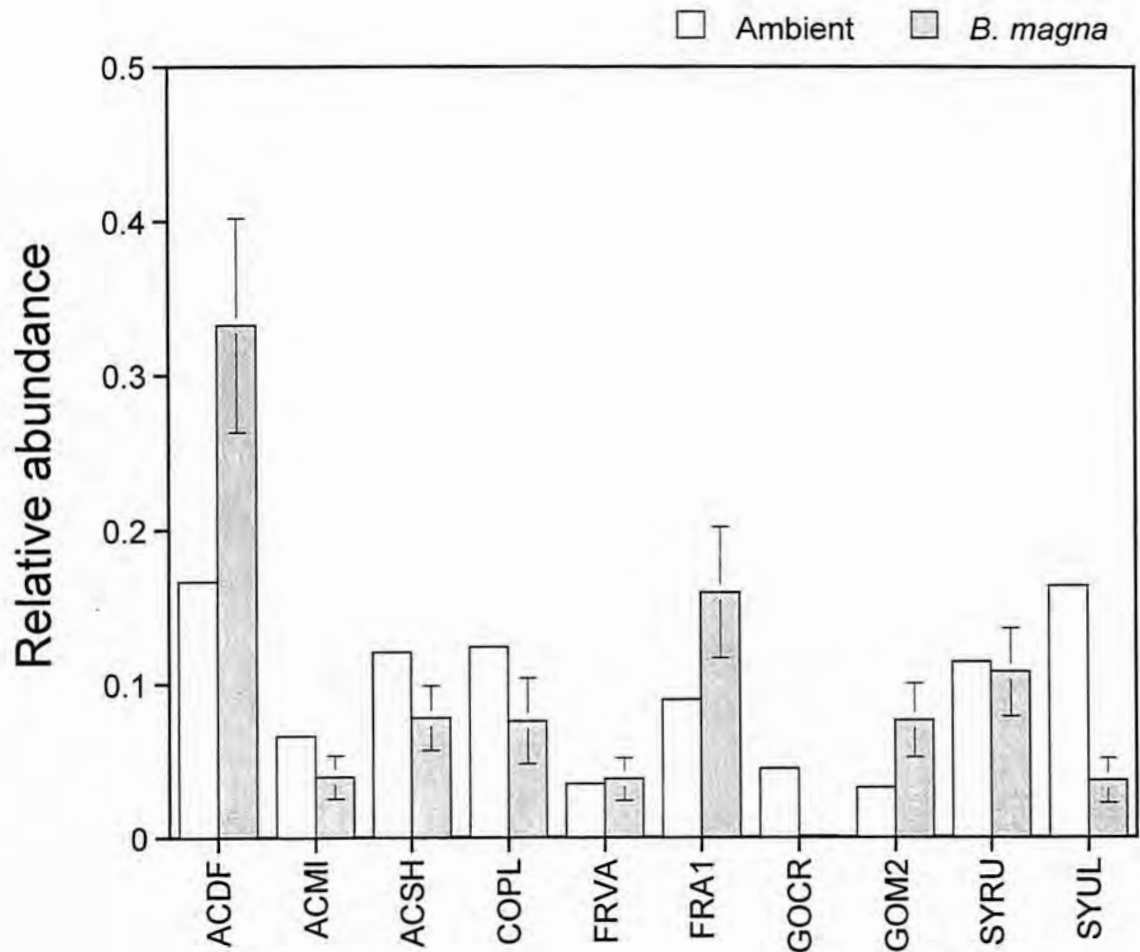
Fig. 2. Frequency histogram comparing relative abundance of major diatom taxa in ambient algal assemblage and larval gut contents of *B. magna* from Cataloochee Creek, North Carolina, in November, 1998. See Table 3.2 for diatom abbreviations.
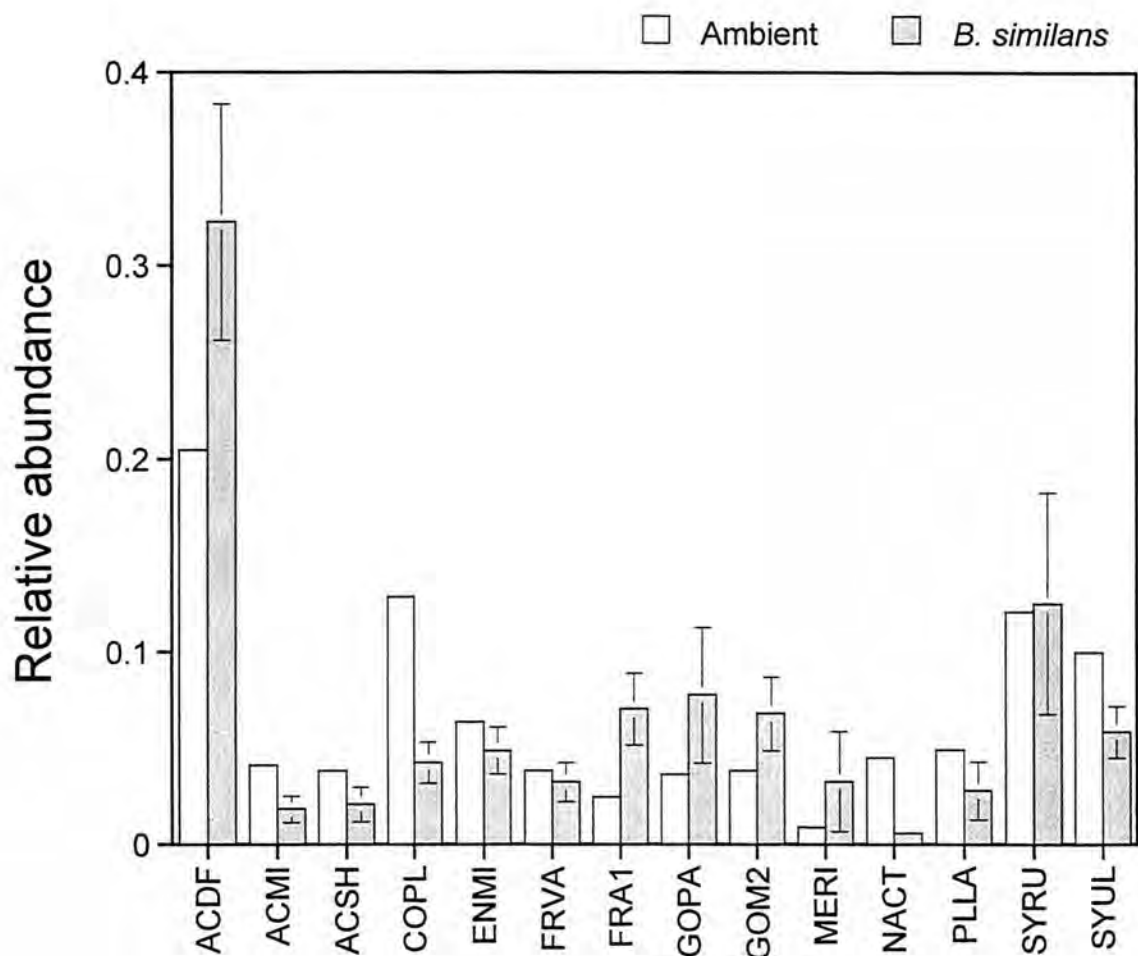
Fig. 3. Frequency histogram comparing relative abundance of major diatom taxa in ambient algal assemblage and larval gut contents of *B. magna* from Cataloochee Creek, North Carolina, in December, 1998. See Table 3.2 for diatom abbreviations.

Fig. 4. Frequency histogram comparing relative abundance of major diatom taxa in ambient algal assemblage and larval gut contents of *B. similans* from Cataloochee Creek, North Carolina, in June, 1999. See Table 3.2 for diatom abbreviations.
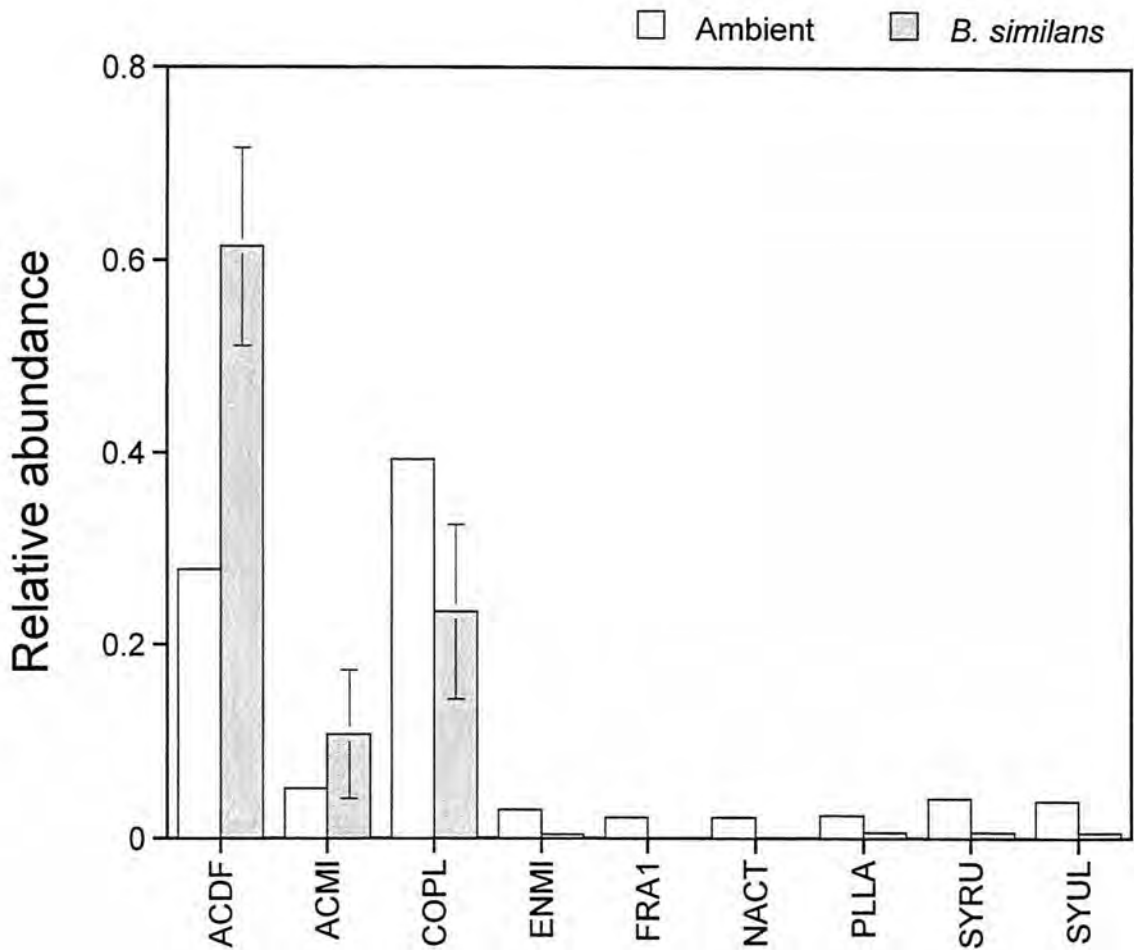
Fig. 5. Frequency histogram comparing relative abundance of major diatom taxa in ambient algal assemblage and larval gut contents of *B. similans* from Cataloochee Creek, North Carolina, in July, 1999. See Table 3.2 for diatom abbreviations.
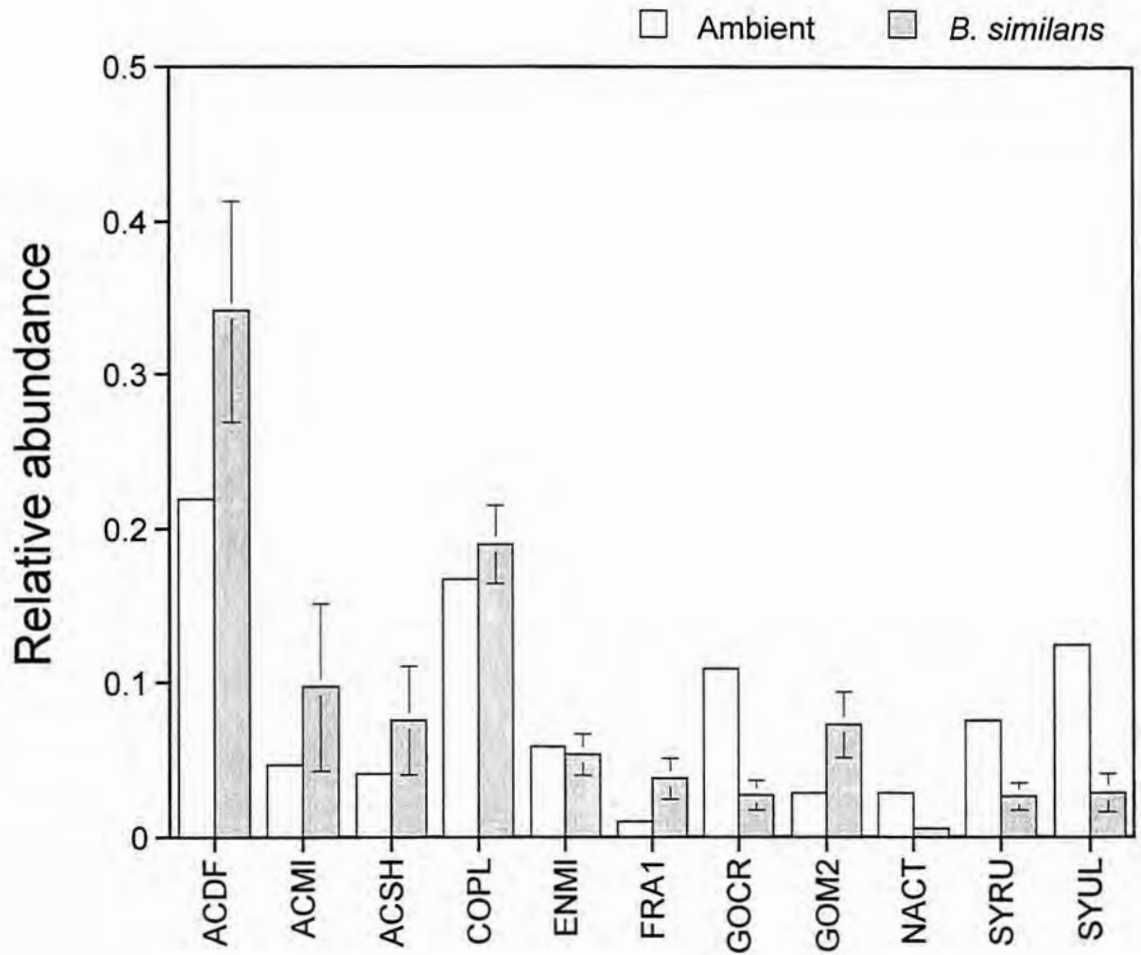
Fig. 6. Frequency histogram comparing relative abundance of major diatom taxa in ambient algal assemblage and larval gut contents of *B. similans* from Cataloochee Creek, North Carolina, in August, 1999. See Table 3.2 for diatom abbreviations.

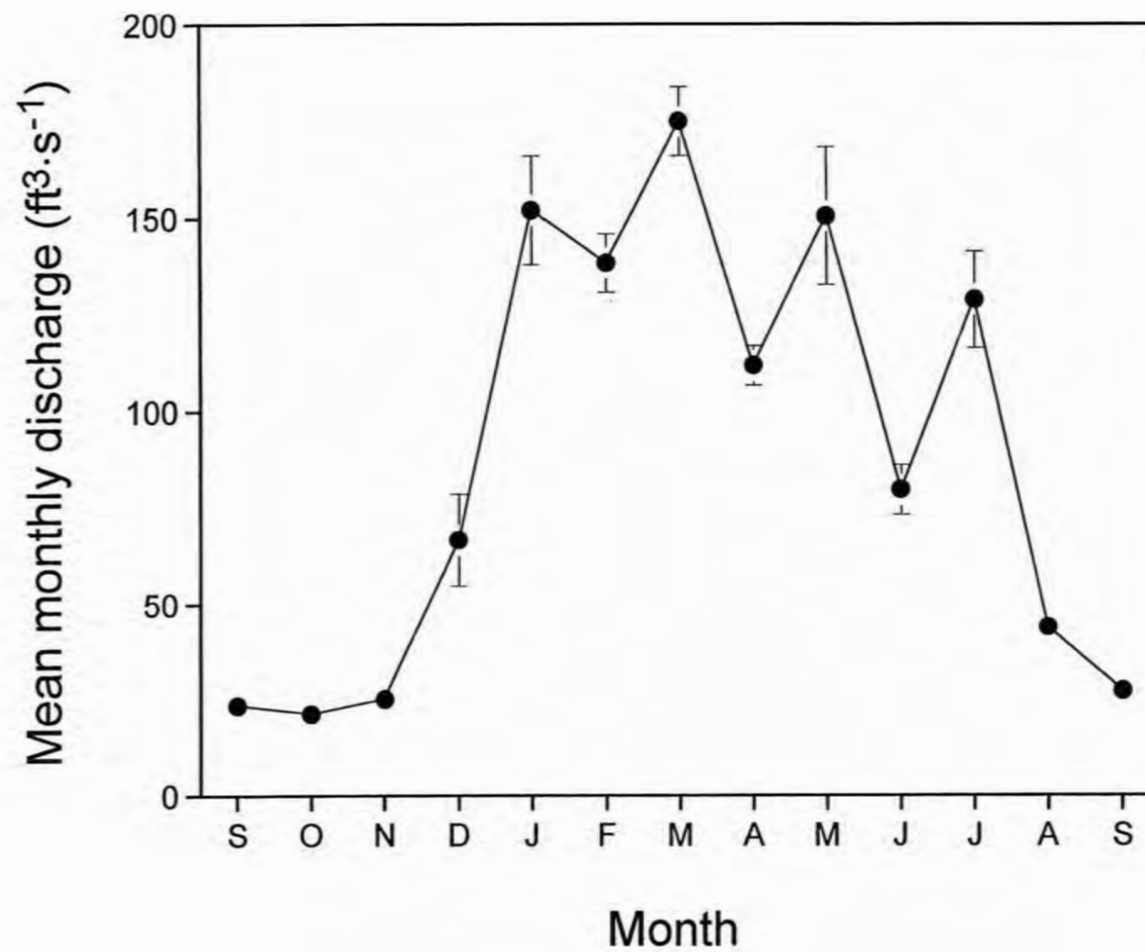# APPENDIX D. MONTHLY DISCHARGE DATA FOR CATALOOCHEE CREEK, NORTH CAROLINA

Fig. 1. Mean monthly discharge (±1 SE) of Cataloochee Creek, North Carolina from September, 1998, through September, 1999. Data were compiled from United States Geological Society gauging station #03460000.

APPENDIX E. ACCOMPANYING COMPACT DISC AND RELEVANT TECHNICAL INFORMATION

System requirements for compact disc:

> *For IBM PC or compatibles.*—Any IBM-compatible machine with an 80286 processor or higher; a CD-ROM drive; a hard disk; EGA or VGA graphics display; ≥12 megabytes of memory; MS-DOS version 3.1 or later and Microsoft Windows version 3.1 or later.
>
> *For Macintosh.*—A Macintosh computer with hard disk; a CD-ROM drive; ≥4 megabytes of memory; Macintosh System 7.0 or later.

Contents of compact disc:

> Compact disc contains data collected and used in analyses for this thesis. Each file contains a single matrix of raw counts of diatom valves for the identified larval group. See Materials and Methods in Chapter 2 or Chapter 3 for additional details.