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Author: Furey, Paula C

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Midges, *Cladophora*, and epiphytes: shifting interactions through succession

Paula C. Furey[1]
Department of Integrative Biology, University of California, Berkeley, California 94720-3140 USA

Rex L. Lowe[2]
Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43402 USA

Mary E. Power[3] **AND Alexis M. Campbell-Craven**[4]
Department of Integrative Biology, University of California, Berkeley, California 94720-3140 USA

Abstract. Midge larvae (*Pseudochironomus richardsoni* Malloch) in the South Fork Eel River, California, weave retreats in mats of *Cladophora glomerata* (L.) Kütz. and graze on its algal epiphytes. Densities of these midges and their effects on *Cladophora* vary over time (seasonally, over the course of succession, and interannually) and space (down the drainage network). New *Cladophora* growth is green, turns yellow with early colonization by a monolayer of *Cocconeis*, and rusty-red as it becomes heavily epiphytized by a multistory layer of *Epithemia* spp. (Rhopalodiaceae), diatoms that contain N-fixing endosymbiotic cyanobacteria. To determine how midges influence epiphyte assemblage structure, we incubated *Cladophora* in early (green [G]), mid (yellow [Y]), and late (rusty-red [R]) stages of succession with and without midges and assessed changes in epiphyte density and composition. Midge effects on epiphyte composition and density (as measured by % cover on *Cladophora* filaments) varied with stage of succession and proximity to the ends of midge retreats. Local increases in retreat-associated cyanobacteria occurred in Y and R stages. Percent cover of *Cocconeis* increased on Y filaments >2 cm from midge retreats (ambient) indicating indirect midge effects (e.g., fertilization). Midges were less effective grazers on adnate *Cocconeis* cells than on loosely attached *Epithemia* and often ingested *Cladophora* in the process of grazing or retreat building, especially in G and Y stages. In contrast, midges that grazed on R *Cladophora* primarily consumed diatoms in the Rhopalodiaceae. Midge survival and retreat quality were lower in G than in Y or R stages, where retreats were longer and denser. Shifts in epiphyte composition and % cover caused by midge–algae interactions at small scales (μm–m) could affect ecologically significant processes, such as N-fixation and foodweb interactions at larger reach and watershed scales.

Key words: algal–grazer interactions, *Cladophora*, *Cocconeis*, cyanobacteria, diatoms, *Epithemia*, food webs, midge, Mediterranean climate, nitrogen fixation, *Pseudochironomus*.

Small-scale variation in the quality and quantity of periphyton can influence the structure and function of river ecosystems at larger scales by affecting biogeochemical cycling and interactions with higher trophic levels (Power 1992b, Wetzel 1993, Kim and Richardson 2000, Romaní et al. 2004). The composition and density of algal assemblages can vary over small spatial scales (μm–mm) with microenvironmental variation in light, flow, substrate topography, nutrients, or moisture (Krejci and Lowe 1986, Furey et al. 2007, Lowe et al. 2007, Villeneuve et al. 2010). The patchy distributions of periphyton in riverine benthic environments (Henry and Fisher 2003, Soininen 2003, Veselá 2009) also result in part from complex and varied interactions with grazers (Feminella and Hawkins 1995, Liess and Hillebrand 2004). Grazers can alter algal composition and density directly by grazing (Steinman et al. 1987, Hillebrand 2002, 2008) or indirectly via excretion (Hillebrand et al. 2002). Reciprocally, variation in periphyton composition and density can affect grazer fitness and survival, i.e., via

[1] Present address: Department of Biology, Saint Catherine University, St. Paul, Minnesota 55105 USA. E-mail: pcfurey@hotmail.com

[2] E-mail addresses: lowe@bgsu.edu

[3] mepower@berkeley.edu

[4] acampbellcraven@gmail.com

differences in the quality and quantity of food (Gresens 1997, Hessen et al. 2002) or by providing refuge. Thus, grazer–periphyton interactions in rivers may have strong ecological consequences for foodweb dynamics and biogeochemical processes at reach and watershed scales. Understanding ecological linkages that cross scales (both temporally and spatially) will strengthen our ability to predict ecosystem response to environmental changes.

In the South Fork of the Eel River, California, spatial (down the drainage network) and temporal (seasonal and interannual) variation in grazer–algae interactions can significantly influence the amount and distribution of algal biomass (Finlay et al. 2002, Power et al. 2008). The Eel River is an N-limited river in a Mediterranean climate. Most rain falls between October and April, and interannual variation in the magnitude and frequency of floods significantly influences algae–grazer dynamics in summer (Power et al. 2008). After winters with scouring floods, densities of a large voracious caddisfly, *Dicosmoecus gilvipes* (Hagen), are reduced, releasing the filamentous green alga, *Cladophora glomerata* (L.) Kütz., from grazing pressure (Power 1990b, 1992a). Subsequent proliferations of *Cladophora* filaments, often several meters in length, can increase the surface area available to algal epiphytes up to 200,000× over plan-view (water surface) area (Power et al. 2009).

Epiphyte assemblages on *Cladophora* vary seasonally and spatially down the drainage network, e.g., as light, flow, and substrate change (Power 1990a, b, Bergey et al. 1995, Power et al. 2009). In early summer, new *Cladophora* growth is green with a light load of algal epiphytes, which generally include stalked diatoms, such as *Gomphonema* Ehrenb. and *Rhoicosphenia* Grunow. By mid-summer, *Cladophora* turns yellow because of colonization by a dense monolayer dominated by the adnate diatom *Cocconeis pediculus* Ehrenberg. This mid-successional epiphyte assemblage changes to a rusty-red multistory epiphyte assemblage dominated by diatoms in the Rhopalodiaceae, especially *Epithemia sorex* Kütz. and *Epithemia turgida* (Ehrenb.) Kütz, but also *Epithemia adnata* (Kütz.) Bréb. and *Rhopalodia gibba* (Ehrenb.) O. Müller. This unique group of diatoms contains N-fixing endosymbiotic cyanobacteria (Floener and Bothe 1980, DeYoe et al. 1992). *Epithemia*-covered *Cladophora* can elevate rates of N-fixation, increasing the biologically available N in the river (J. Welter, St. Catherine University, unpublished data), especially in reaches draining >100 km^2, where *Cladophora* and its epiphytes dominate the summer biomass of primary producers (Power et al. 2009). Spatial and temporal variation in densities and distribution of loosely vs tightly attached algal epiphytes and N-fixing taxa probably influence the quality and quantity of algal food available to grazers (McCormick and Stevenson 1989, Dudley 1992).

Larvae of the herbivorous midge, *Pseudochironomus richardsoni*, weave retreats from *Cladophora* and graze on its algal epiphytes, primarily diatoms (Power 1991, Gresens 1997, Power et al. 2009). Initially, retreat weaving by midges reduces *Cladophora* biomass through clipping and fragmentation (Power 1990a), but midge grazing grooms epiphytes from underlying *Cladophora* (fig. 6 in Power et al. 2009), enhancing its exposure to light and nutrient fluxes. These observations suggest a complex interaction between midges, *Cladophora*, and its associated epiphytes. However, little is known about how grazing by midges changes local algal assemblage composition and densities, especially of N-fixing Rhopalodiaceae. *Cladophora* proliferations and retreat-weaving midges are widespread and abundant in the Eel and similar rivers, so they could have large ecological and biogeochemical effects at basin scales, if midge–*Cladophora* interactions significantly alter epiphyte composition.

We examined effects of *P. richardsoni* on the composition and % cover of epiphytic assemblages on *Cladophora* in early (green [G]), mid (yellow [Y]), and late (rusty-red [R]) stages of succession, with special focus on N-fixing diatoms in the Rhopalodiaceae. We also examined midge retreats (length, density of retreat walls, construction rates) built with *Cladophora* filaments in these 3 stages. We hypothesized that retreat-weaving midges would change the composition and % cover of epiphytic assemblages on *Cladophora* in areas near or associated with their retreats by decreasing the densities of N-fixing diatoms like *Epithemia* and upright diatoms like *Rhoicosphenia.* We expected these taxa to be more common in midge guts relative to adnate diatoms like *Cocconeis*. Second, we hypothesized that *Cladophora* health, as measured by chloroplast vigor, would increase in the presence of midges if midges reduced epiphyte loads and exposed underlying *Cladophora* to increased light and water-column nutrients. We expected this facilitation would be stronger in R *Cladophora* with more loosely attached epiphytes than in G *Cladophora* with light epiphyte loads or in Y *Cladophora* with dense loads of the *Cocconeis,* predicted to be more difficult to graze.

Methods

We collected midges (*P. richardsoni*) and algae (*C. glomerata* and associated epiphytes) on 13 July 2009 from the South Fork of the Eel River in the Angelo

Coast Range Reserve, Mendocino County, California, USA (lat 39°43′45″N, long 123°38′45″W; http://angelo.berkeley.edu). Midges were collected from R *Cladophora* from the same reach with similar habitat conditions (light, substrate, flow). We incubated *Cladophora* with epiphyte assemblages indicative of the 3 different successional stages (G, Y, R stages) at room temperature (20–23°C) in the laboratory in Petri plates (8.9 cm diameter) in the presence and absence of midges (2 × 3 factorial design, 6 replicates). River temperatures during this time ranged from 19.5 to 21.0°C. Temperature in the laboratory, which lacked heat or air conditioning and was within the riparian corridor <100 m from the river, was similar to temperature at the river–air interface during July and August, when midge abundance was highest. Lack of flow in the Petri plates was of potential concern as a laboratory artifact. However, the short (~2-d) duration of the incubation, the low biomass density of *Cladophora* in the Petri plates, refreshment of water in the Petri plates, and the partial similarity of laboratory to field conditions somewhat reduced these concerns. During the low-flow summer period, floating *Cladophora*, its epiphytes, and heavy midge infestations commonly occur in stagnant backwaters and along pool margins where flow is minimal. Petri plates were incubated next to a corner of windows (facing north and west), where they received ambient sunlight filtered through forest. We added river water daily as needed.

We removed insects and debris from freshly gathered *Cladophora* with gentle rinsing and by picking with forceps. We held cleaned *Cladophora* samples in a 0.3-mm-mesh net to allow excess water to drain for 30 s before weighing to obtain damp mass. We added 0.76 ± 0.08 g (mean ± SE) damp mass to each Petri plate and filled each Petri plate with river water. We laid plates out in a randomized blocked design with different treatments cross-grouped by the 3 successional stages (and corresponding epiphyte loads) of *Cladophora* and the presence or absence of midges. Before we added midges, we determined epiphyte densities from samples of algae from each Petri plate (*see below*). We gently teased midges from their retreats and added 3 midges (8.0–11.2 mm body length) to each with-midge Petri plate. We ran the experiment until midges were preparing to pupate (indicated by an enlarged thorax) (52 h). At hour 22 we replaced any midges that had died.

We assessed retreat robustness at hours 9, 19, 23, 31, and 52. We measured retreat length and scored retreat-wall density on a relative scale: 1 = little to no weaving of *Cladophora* filaments, 2 = light weaving, bottom of the Petri plate easily visible through much of the retreat, 3 = <50% of the bottom of the Petri plate visible, 4 = <80% of the bottom of the Petri plate visible, 5 = could not see through retreat.

At the end of the experiment, we scored the overall percentages of healthy vs unhealthy *Cladophora* (as determined by changes in color and texture and the presence of any surface films that developed on the water). We compared chloroplast health between the beginning and the end of the experiment by assessing the fullness of unpreserved *Cladophora* cells along filaments. We scored cell fullness/chloroplast health on a relative scale (5 = very healthy, bright green chloroplast that filled 95 to 100% of the cell, 4 = healthy chloroplast that filled 70 to 94% of the cell, 3 = chloroplast filled 40 to 69% of the cell, 2 = chloroplast not healthy and filled 20 to 39% of the cell, 1 = chloroplast filled <20% of the cell or only remnants of the chloroplast present, 0 = cell appeared to be dead). We preserved (2% formaldehyde) algae collected from the middle of the Petri plate in control treatments, and algae collected >2 cm from both ends of midge retreats (not associated with retreats; ambient algae) and <0.2 cm from retreat ends (retreat-associated) from each with-midge treatment (retreats made by midges that had been replaced were not selected). We collected and preserved material from midge fore- and hindguts. We preserved 2 retreats from each of the G, Y, and R treatments in 2% formaldehyde for scanning electron microscope (SEM) analysis. Retreats from G treatments did not maintain sufficient structure and were not analyzed under the SEM.

Algal analysis

We counted 10 Whipple-grid views (10 × 10 squares; square width = 12 μm) for each algal sample at 500× (400× with a 1.25 optivar) using a Nikon Optiphot photomicroscope with Nomarski differential interference contrast optics (Nikon Co., Tokyo, Japan). The Whipple-grid method of counting allowed us to take into account differences in biovolume among algal species. We determined epiphyte loads (% cover) by lining up *Cladophora* filaments horizontally under a Whipple-grid and counting only the epiphytes on the upper surface and half way down the curve on each side of a filament (½ of the cylindrical filament). When the width of the *Cladophora* filament was less than the width of the Whipple grid, we normalized filament width to 100% of the Whipple-grid area by applying a correction factor. The cyanobacterium *Chamaesiphon* Braun *et* Grunow

was too small to estimate accurately by this method, so we counted each *Chamaesiphon* cell and divided the total count by 10 to establish a *Chamaesiphon* areal-equivalency unit for data analyses (i.e., 10 *Chamaesiphon* cells = 1 *Chamaesiphon* unit). In addition, we used the cell counts to calculate *Chamaesiphon* density/*Cladophora* surface area (cells/cm^2). Relative biovolume of epiphytes was also calculated. For midge gut analyses, we used the Whipple grid to count live and dead cells, including broken parts of diatoms when >25% of the frustule was present.

We processed midge retreats for SEM analysis through an alcohol series to remove water prior to critical-point drying (Samdri-780A Critical Point Dryer; Tousimis Research Corp., Rockville, Maryland). We sectioned samples with a sharp razor blade and mounted the sections on aluminum SEM stubs with the aid of a dissecting microscope to establish retreat orientation. We sputter-coated midge retreats with 10 nm of AuPd and examined and photographed them under a high-resolution Hitachi S2700 SEM (Hitachi Co., Tokyo, Japan).

Data analysis

For epiphyte assemblage analysis, we normalized % cover with an arcsine$\sqrt{(x)}$ transformation (appropriate for proportional data) and examined clustering based on a reduced taxon list with nonmetric multidimensional scaling (NMDS) of Bray–Curtis similarities (Primer 5, version 5.2.9; Primer-E Ltd., Ambleside, UK; Clarke 1993). We excluded taxa that were present in only 1 or 2 Petri plates to ensure sufficient data for ordination. We examined NMDS clustering patterns of ambient algae based on *Cladophora* stage (G, Y, R), time (beginning and end of the experiment), presence/absence of midges, and combinations of these variables. We examined the effect of midges on epiphyte assemblage structures closer to the midge retreats (a more local effect) by including epiphyte assemblages on retreat-associated *Cladophora* and using position (ambient and retreat-associated) as an additional factor. We derived Analysis of Similarity (ANOSIM) routines from the Bray–Curtis similarity matrix to determine whether % cover of taxa in epiphyte assemblages differed in the presence and absence of midges at the beginning and end of the experiment or between epiphyte assemblages from retreat-associated and ambient algae. When significant differences were detected, we conducted post hoc pairwise comparisons and explored the *R* values of the pairwise comparisons (larger values indicate greater segregation of samples). We applied Bonferroni corrections to account for multiple comparisons.

To examine the grazing preferences of midges for a particular algal type i out of m possible algal food types in the environment, we used Chesson's (1978, 1983) food preference index:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}$$

where α_i is the estimated preference for algal food type i, r_i is the abundance of the i^{th} food type in the diet, n_i is the abundance of the i^{th} food type in the environment, scaled so that α_i for all available food types in the environment sum to 1. We used Chesson's (1983) model, which assumed no food depletion. We assumed that consumed epiphytic algae were replaced by reproduction or that the difference over 2 d was insignificant relative to total epiphytic algal biomass. Midges may have reduced algal cell densities on a local microscale, but algae did not look visibly depleted of epiphytes.

We used a 2-way analysis of variance (ANOVA) to determine if change in chloroplast health of *Cladophora* between the beginning and end of the experiment was affected by the presence/absence of midges, *Cladophora* stage, or the interaction of these 2 factors. We ran Tukey's post hoc multiple comparisons with a Bonferroni-corrected *p*-value when we found significant differences among means. We used repeated measures analysis of variance (RM ANOVA) with 1 within-subjects factor (time) and 1 between-subjects factor (*Cladophora* stage) to test whether retreat length or density score differed with time or *Cladophora* stage. We used retreat measurements made on all 4 dates. We used an ANOVA with Tukey's post hoc comparisons to test for differences over time and between retreat ends and ambient algae in mean *Chamaesiphon* cell densities on Y *Cladophora*. We did all ANOVA and RM ANOVA statistical procedures with SPSS (version 16.0; SPSS, Chicago, Illinois).

Results

Algal assemblages

The composition of ambient epiphyte assemblages differed significantly among G, Y, and R *Cladophora* stages (ANOSIM$_1$, global $R = 0.803$, $p = 0.001$; Table 1). Within each *Cladophora* stage, epiphyte assemblages in control and midge plates were similar at the start of the experiment (though they were variable) but changed over time (duration of the experiment) or in the presence of midges (ANOSIM$_1$; Tables 1, 2, Fig. 1A–C). G *Cladophora* had diverse but

TABLE 1. Post hoc comparisons from Analysis of Similarity (ANOSIM) derived from the Bray–Curtis similarity matrix of arcsine$\sqrt{(x)}$-transformed % cover of epiphytic algal taxa. The 1st ANOSIM ($ANOSIM_1$) examines broader midge effects on epiphytes by comparing epiphyte assemblages from the ambient *Cladophora* in the presence of midges (Midge) with epiphyte assemblages in the absence of midges (Control) from the beginning (Before) and end (After) of the experiment for green, yellow, and rusty-red *Cladophora* stages (see Fig. 1A–C). The 2nd ANOSIM ($ANOSIM_2$) examines more local midge effects by comparing epiphyte assemblages from ambient *Cladophora* in midge treatments with retreat-associated epiphyte assemblages for *Cladophora* stages (see Fig. 3A–C). The p value for the post hoc comparisons was adjusted to $p < 0.0042$ ($ANOSIM_1$) and $p < 0.0167$ ($ANOSIM_2$) to account for multiple comparisons. Significant p values are underlined.

	Ambient algae				
Cladophora color	Treatment			R	p
$ANOSIM_1$: Global $R = 0.803$, $p = 0.001$; post hoc: $p < 0.0042$					
Green	Before-control	vs	Before-midge	0.291	0.150
	Before-control	vs	After-control	0.640	<u>0.002</u>
	Before-midge	vs	After-midge	0.409	<u>0.002</u>
	After-control	vs	After-midge	0.463	0.011
Yellow	Before-control	vs	Before-midge	0.048	0.281
	Before-control	vs	After-control	0.298	<u>0.004</u>
	Before-midge	vs	After-midge	0.596	<u>0.002</u>
	After-control	vs	After-midge	0.435	<u>0.002</u>
Rusty-red	Before-control	vs	Before-midge	−0.007	0.494
	Before-control	vs	After-control	0.756	<u>0.002</u>
	Before-midge	vs	After-midge	0.952	<u>0.002</u>
	After-control	vs	After-midge	−0.080	0.740
$ANOSIM_2$: Global $R = 0.807$, $p = 0.001$; post hoc: $p < 0.0167$					
Green	After-midge	vs	Retreat-associated	0.174	0.088
Yellow	After-midge	vs	Retreat-associated	0.536	<u>0.001</u>
Rusty-red	After-midge	vs	Retreat-associated	0.340	<u>0.001</u>

low % cover of epiphytes, of which *Cocconeis* and *Rhoicosphenia* were most common (Table 2). Y *Cladophora* had a denser load of epiphytes dominated by a monolayer of *Cocconeis* (>95% relative biovolume), primarily *Cocconeis pediculus* (Table 2, Fig. 2A–D). R *Cladophora* had a multilayered (2–3 layers) load of epiphytes, rich in N-fixing taxa, and predominantly diatoms in the Rhopalodiaceae (>50% relative biovolume), especially *E. sorex* and *E. turgida* (Table 2, Fig. 2E, F, H). Chlorophytes on R *Cladophora* were dominated by *Gongrosira*, a taxon that was absent from G or Y successional stages. Over time, % cover of *C. pediculus* increased on G *Cladophora* in the control and on Y *Cladophora* in the presence of midges and at retreats ends (Table 2). Over time, % cover of Rhopalodiaceae and N-fixing cyanobacteria increased on R *Cladophora* in the control and midge treatments and on retreat ends (Table 2). The insides of Y and R retreats were lined with silk and absent of epiphytes (Fig. 2 C, G).

Midges affected % cover of the epiphyte assemblages on ambient Y but not G or R *Cladophora* (broader midge effect, $ANOSIM_1$, after-control vs after-midge pairwise comparisons, $p < 0.0042$; Fig. 1, Table 1). Percent cover of *C. pediculus* on ambient Y *Cladophora* increased more with midges than in their absence (Table 2). No significant difference in overall epiphyte assemblage structure on G *Cladophora* was detected in the presence and absence of midges ($ANOSIM_1$; Table 1).

Midges significantly altered the composition and % cover of epiphytes on retreat-associated *Cladophora* compared to on ambient *Cladophora* in the Y and R stages, but not in the G stage ($ANOSIM_2$, global $R = 0.807$, $p = 0.001$, pairwise comparisons, $p < 0.0167$; Fig. 3A–C, Table 1). On Y *Cladophora*, % cover of *Cocconeis* (Table 2) was lower and % cover and density of *Chamaesiphon* were greater on retreat-associated filaments than on ambient filaments (Tables 2, 3). *Chamaesiphon* densities were 9× higher on retreat-associated than on ambient *Cladophora* (Table 3). On R *Cladophora*, % cover of cyanobacteria (especially N-fixing cyanobacteria such as *Calothrix*) was greater on retreat-associated than on ambient filaments (Table 2). Except for *Chamaesiphon*, cyanobacteria generally were absent or present in lower numbers on Y and G than on R *Cladophora* (Table 2). On R *Cladophora*, *Chamaesiphon* was found only on retreats (Tables 2, 3). Percent cover of *Cocconeis* was slightly higher on retreat-associated than on ambient R *Cladophora*, but overall densities of Rhopalodiaceae were similar between control, ambient midge, and

Table 2. Mean % cover and relative biovolume of epiphytic algae on green, yellow, and rusty-red *Cladophora* from the beginning (Before) and end (After) of the experiment from treatments with midges (Midge) and without midges (Ctrl) and from the ends of midge retreats (Rtrt = retreat-associated). Cyano = cyanobacteria, Chl = Chlorophyta, F = N fixer, X = non-N-fixer.

			Green					Yellow					Rusty–red				
			Before		After			Before		After			Before		After		
Algal division	F/X	Taxonomic grouping[a]	Ctrl	Midge	Ctrl	Midge	Rtrt	Ctrl	Midge	Ctrl	Midge	Rtrt	Ctrl	Midge	Ctrl	Midge	Rtrt
% cover																	
Diatoms	F	Rhopalodiaceae	–	0.2	0.1	0.1	0.1	0.1	–	0.5	0.3	0.2	5.9	7.0	20.3	20.1	20.9
Diatoms	X	*Cocconeis*	1.6	0.9	8.4	2.9	2.5	38.5	36.3	38.1	52.9	41.9	1.6	1.8	0.9	0.4	3.5
Diatoms	X	*Rhoicosphenia*	0.2	3.3	0.5	1.0	0.8	0.1	0.2	0.3	0.2	0.2	1.4	1.5	1.4	1.4	1.6
Diatoms	X	Other diatoms	0.0	0.2	0.0	0.3	0.0	0.1	0.1	0.2	0.1	0.1	0.3	0.3	0.2	0.6	1.0
Cyano	F	N-fixing cyanobacteria	–	–	–	–	–	–	–	–	–	–	–	–	0.3	0.3	1.8
Cyano	X	*Chamaesiphon*	–	–	–	–	–	1.3	0.3	0.6	0.2	1.5	–	–	–	–	0.1
Cyano	X	Other cyanobacteria	–	–	–	–	–	0.1	0.1	–	–	–	0.5	0.3	0.4	0.2	1.4
Chl	X	Chlorophyta	–	–	–	–	0.1	0.1	0.1	0.0	0.4	0.2	1.6	0.1	2.3	2.4	2.0
		Total	1.8	4.5	9.1	4.2	3.5	40.1	37.0	39.7	54.1	44.0	11.2	11.0	25.8	25.3	32.3
Relative biovolume																	
Diatoms	F	Rhopalodiaceae	–	3.3	1.5	1.2	3.1	0.1	–	1.1	0.5	0.4	52.1	62.8	77.8	77.8	64.8
Diatoms	X	*Cocconeis*	86.4	20.4	92.8	69.2	73.2	95.4	97.7	95.8	97.7	95.3	13.8	16.0	3.3	1.4	10.8
Diatoms	X	*Rhoicosphenia*	12.7	72.9	5.7	22.9	22.2	0.2	0.4	0.8	0.4	0.4	12.1	13.7	5.4	5.5	4.8
Diatoms	X	Other diatoms	0.9	3.3	0.0	6.7	0.0	0.7	0.8	0.6	0.4	0.2	4.1	4.0	1.7	4.3	3.1
Cyano	F	N-fixing Cyanobacteria	–	–	–	–	–	–	–	–	–	–	–	–	1.3	1.2	5.5
Cyano	X	*Chamaesiphon*	–	–	–	–	–	3.2	0.7	1.6	0.3	3.3	–	–	–	–	0.4
Cyano	X	Other cyanobacteria	–	–	–	–	–	0.1	0.1	–	–	–	4.0	2.8	1.7	0.7	4.4
Chl	X	Chlorophyta	–	–	–	–	1.4	0.4	0.2	0.1	0.8	0.4	14.0	0.6	8.8	9.1	6.2

[a] Rhopalodiaceae = *Epithemia adnata*, *Epithemia sorex*, *Epithemia turgida*, and *Rhopalodia gibba*; *Cocconeis* = *C. pediculus* and *C. placentula*; other diatoms = *Achnanthidium minutissima* (Kütz.) Czarnecki, *Cymbella* spp., *Fragilaria* spp., *Gomphonema* spp., *Navicula* spp., *Nitzschia* spp., *Melosira* sp., *Synedra* spp., and miscellaneous other diatoms; N-fixing cyanobacteria = *Calothrix* spp., *Stigonema* spp., *Tolypothrix* spp.; other (non-N-fixer) cyanobacteria = Oscillatoriaceae, *Gloeothece* sp.; Chlorophyta = *Aphanochaete* sp., *Ankistrodesmus* sp., *Bulbochaete* sp., *Characium* sp., *Gongrosira* sp., *Mougeotia* spp., *Oedogonium* spp., and *Ulothrix* sp.

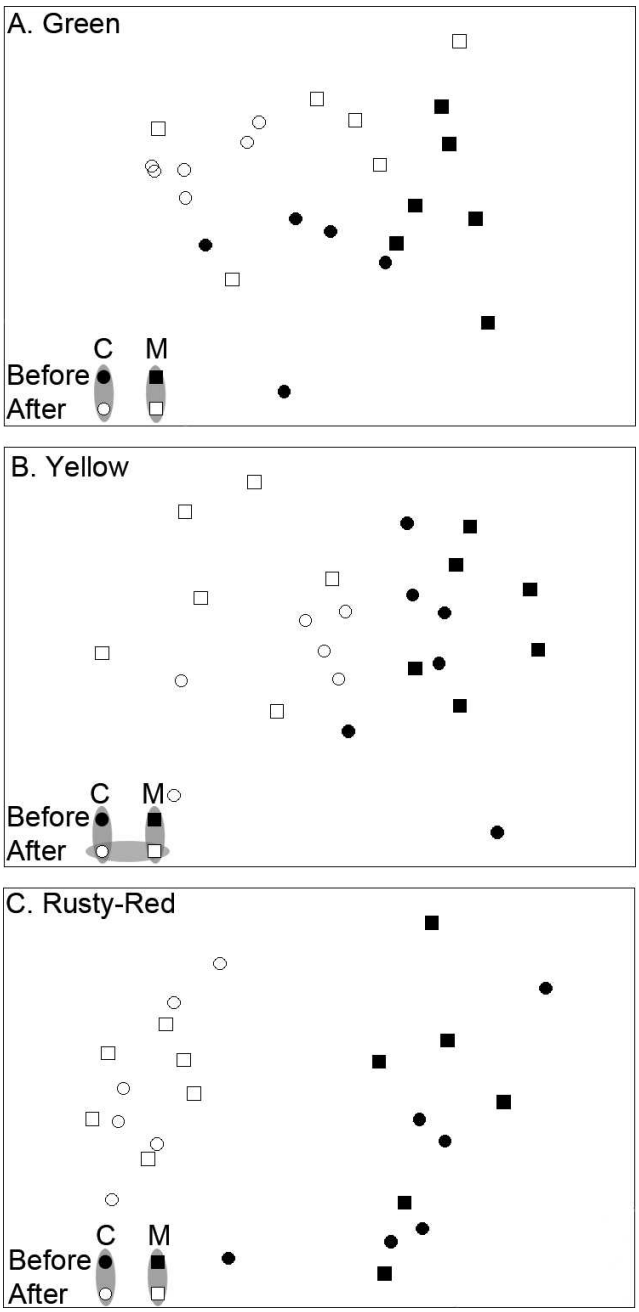

FIG. 1. Two-dimensional nonmetric multidimensional scaling ordination of Bray–Curtis similarities from arcsine$\sqrt{(x)}$-transformed % cover of epiphytic algae on green (A), yellow (B), and rusty-red (C) *Cladophora* from the beginning (before) and end (after) of the experiment in the absence (C) and presence (M) of midges. In the key to symbols, assemblages from treatment combinations circled in gray are statistically different ($ANOSIM_1$, post hoc pairwise comparisons $p < 0.0042$; Table 1).

retreat-associated filaments (Table 2). SEM micrographs of retreats constructed of Y *Cladophora* did not show any filaments at the retreat opening or mid retreat that were notably cleared of epiphytes (Fig. 2A–B), whereas micrographs of retreats constructed of R *Cladophora* showed that some filaments were largely epiphyte-free (Fig. 2E).

Midge gut contents

Live cells (i.e., cells with intact chloroplasts) were predominant in midge foreguts and empty frustules were predominant in hindguts (Table 4). Rhopalodiaceae frustules in the hindgut often contained cyanobacterial endosymbionts, but other cellular contents (i.e., diatom chloroplasts) were absent. Overall, midges showed a dietary preference for diatoms ($\alpha_i > 0.89$) relative to green algae and cyanobacteria (Chesson 1983). Midge intake of *Cocconeis* relative to other diatoms was greater in plates with G *Cladophora*, whereas midges preferentially consumed non-*Cocconeis* diatoms in plates with Y and R *Cladophora* (Table 5). Guts from midges in plates with G *Cladophora* contained a variety of diatoms, including *Cocconeis*, *Rhoicosphenia*, and Rhopalodiaceae taxa (Table 4). Guts from midges in plates with Y *Cladophora* primarily contained *Cocconeis* frustules and some Rhopalodiaceae cells (Table 4). Guts from midges with R *Cladophora* contained >93% Rhopalodiaceae taxa (Table 4). Midges in plates with Y and G *Cladophora* consumed more filamentous green algae, especially *Cladophora* (but α was not high), than midges from plates with R *Cladophora* (Tables 4, 5; PCF, personal observation).

Midge retreats and Cladophora *health*

Midges in plates with G, Y, and R *Cladophora* lined their retreats with woven silk (Fig. 2C, G; no SEM data are available for G *Cladophora*: PCF and AMC-C, personal observation). The density and length of retreats in G, Y, and R stages of *Cladophora* increased significantly with time as midges constructed their retreats (RM $ANOVA_1$, $F_{3,84\ \text{length}} = 7.775$, $F_{3,84\ \text{density}} = 17.960$, $p < 0.000$; Fig. 4A, B). Overall, midges built denser retreats faster in Y and R *Cladophora* than in G *Cladophora*, where density scores were never >3 (Fig. 4B). More midges died in the first 24 h in G (44%) than Y and R *Cladophora* (11%).

Chloroplasts from G *Cladophora* were significantly healthier (vibrant color and higher chloroplast health score) at the beginning than at the end of the experiment and were healthier than chloroplasts in Y and R *Cladophora* regardless of time (ANOVA, $F_{8,62} = 19.82$, $p < 0.05$; Tukey post hoc, $p < 0.004$). Overall,

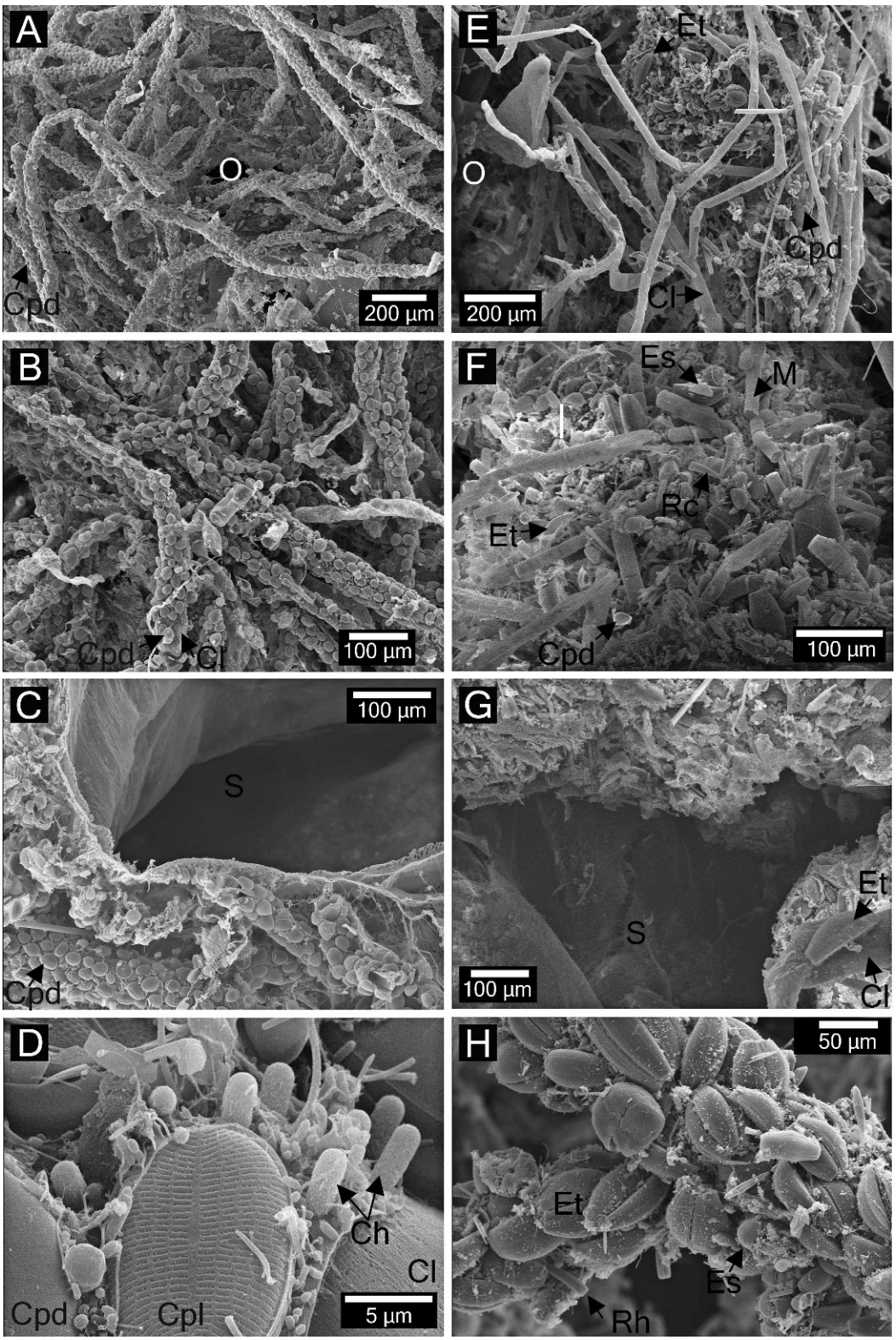

Fig. 2. Scanning electron micrographs of midge retreats constructed from yellow (A–D) and rusty-red (E–H) *Cladophora* filaments. A.—Opening (O) of retreat with *Cocconeis*-dominated *Cladophora* filaments. B.—Outer mid-retreat areas with *Cocconeis*-dominated *Cladophora* filaments. C.—Mid-retreat cross section. Note the paucity of algae on the inner silk lining (S). D.—Close up of a retreat-associated *Cladophora* filament with bacteria and cyanobacteria (including *Chamaesiphon*) at the margins and between

midges exerted a positive effect on the health of *Cladophora*. Less filament discoloration and water film was observed in the presence than in the absence of midges, and the chloroplast health score decreased less between the beginning and end of the experiment in the presence than in the absence of midges (2-way ANOVA with midge presence/absence and *Cladophora* stage as fixed factors, $F_{1,29} = 13.69$, $p < 0.05$). Decreases in *Cladophora* health scores were affected by a significant interaction between presence/absence of midges and *Cladophora* stage (2-way ANOVA, $F_{2,29} = 6.25$, $p < 0.05$). The effect of midges on *Cladophora* health scores was strongest in G *Cladophora*, which in the absence of midges, had notably discolored filaments (80% discolored in the absence of midges vs 20% discolored in the presence of midges; Fig. 5), a film on the water surface, and a significantly greater decrease in *Cladophora* chloroplast health score compared to Y and R *Cladophora* (Tukey post hoc, $p < 0.05$; Fig. 5). This midge effect was present in Y and R *Cladophora* (color change and presence of a surface film on the water) but was less noticeable than in G *Cladophora*, and the change in chloroplast health score was not significant (2-way ANOVA: Tukey post hoc, $p > 0.05$; Fig. 5).

Discussion

The effects of midges on *Cladophora* epiphyte composition and % cover on *Cladophora* differed among successional stages (G, Y, R), as did the spatial scale of midge effects, both local (on retreat-associated algae) and general (on ambient algae >2 cm from retreats). Midges affected epiphyte composition via grazing or incidental consumption during retreat building. Indirect effects of midges could have been mediated through nutrient regeneration and removal of certain epiphytes, which helped maintain *Cladophora* health and released nonselected epiphytes from competition with those that were preferentially grazed.

Direct midge–algae interactions

Midges influenced the composition and % cover of epiphytes by reducing or increasing specific epiphytes on ambient (a broader effect) and on retreat-associated *Cladophora* (a localized effect). Midge effects changed with *Cladophora* stage. On G *Cladophora*, midges affected epiphytes only on ambient filaments, whereas they affected both ambient and retreat-associated Y *Cladophora*, and only retreat-associated R *Cladophora*. Midges preferentially consumed diatoms, as has previously been observed in the Eel River and in other studies (Power 1991, Álvarez and Peckarsky 2005, Power et al. 2009). Midges generally preferentially grazed or consumed upright or nonadnate diatoms relative to tightly attached, adnate cells like *Cocconeis* (Steinman et al. 1987, McCormick and Stevenson 1989, Dudley 1992). In our study, the strength of the midge–algae interactions varied with *Cladophora* stage, evidenced by differences in % cover of upright, loosely attached, and tightly adhered epiphytes among stages.

G Cladophora.—Low densities and patchy distributions of epiphytes on G *Cladophora* made changes in epiphyte % cover and composition difficult to detect. Midges grazed upright or nonadnate taxa, such as *Rhoicosphenia* and *Gomphonema*. Frustules of these genera were found readily in midge guts, and these genera occurred in lower densities on *Cladophora* filaments in the presence than in the absence of midges. The diversity of algal taxa in the midge guts was high, and the density of epiphytic algae available to grazers was low during this early successional stage, and midges appeared to consume all available diatom taxa, including tightly adhered *Cocconeis* cells. Hungry grazers will graze adnate algae more intensively than satiated grazers will (Steinman 1991). Midges attempting to graze *Cocconeis* may have consumed *Cladophora* filaments incidentally because many *Cocconeis* cells present in the midge guts remained attached to *Cladophora* (PCF, personal observation). Midges struggled noticeably to build retreats in G *Cladophora*, and both *Cladophora* and associated *Cocconeis* epiphytes may have been ingested incidentally during construction. Mechanical disturbance during attempts to build cases may have further reduced availability of epiphytes (Cattaneo and Mousseau 1995), although Scrimgeour et al. (1991) found that at low algal densities, algal losses occurred primarily because of consumption rather than mechanical foraging-related causes.

←

Cocconeis cells. E.—Opening (O) of retreat with *Cladophora* filaments with heavy and light epiphyte loads. F.—Outer mid-retreat areas with *Cladophora* filaments with heavy and light epiphyte loads. G.—Mid-retreat cross section. Note the paucity of algae on the inner silk lining (S). H.—Close up of an *Epithemia*-rich, retreat-associated *Cladophora* filament. Ch = *Chamaesiphon*, Cl = *Cladophora*, Cpd = *Cocconeis pediculus*, Cpl = *Cocconeis placentula*, Et = *Epithemia turgida*; Es = *Epithemia sorex*, M = *Melosira*, Rc = *Rhoicosphenia*, Rh = *Rhopalodia*.

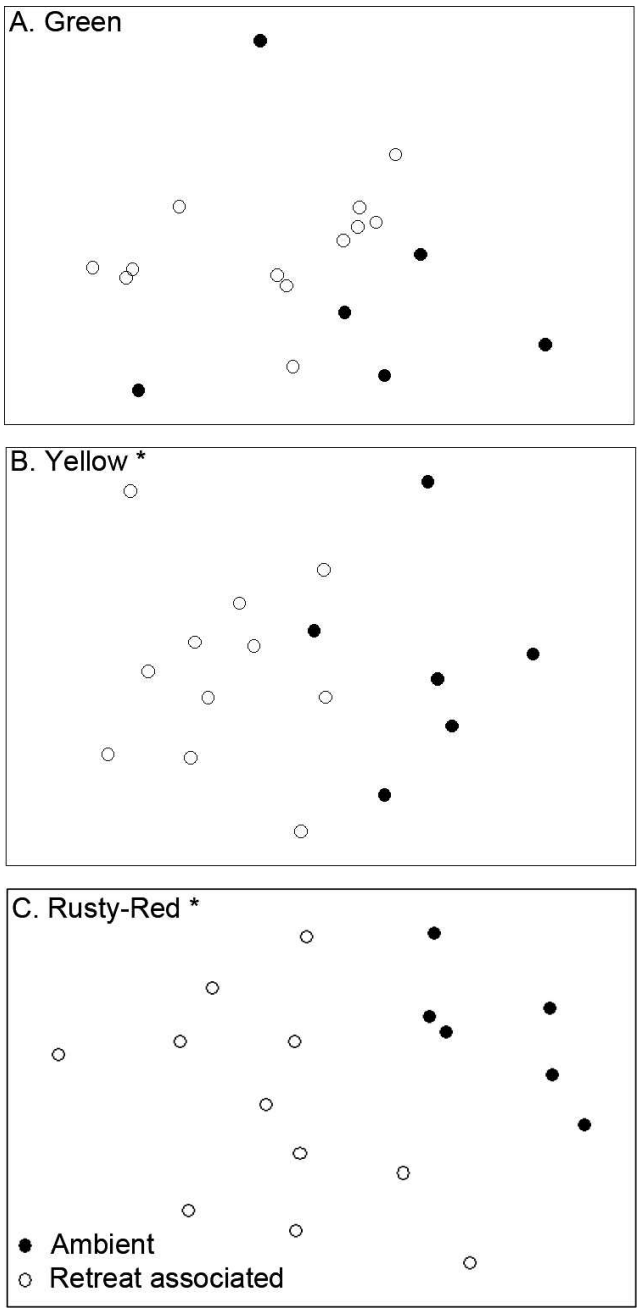

FIG. 3. Two-dimensional nonmetric multidimensional scaling ordination of Bray–Curtis similarities from arcsine$\sqrt{(x)}$-transformed % cover of epiphytes on ambient and retreat-associated green (A), yellow (B), and rusty-red (C) *Cladophora* filaments. Asterisks indicate significant differences ($p < 0.001$). See Table 1 for pairwise comparisons.

Y Cladophora.—Epiphyte assemblages were composed of >95% *Cocconeis* on Y *Cladophora*, and midge guts were full of *Cocconeis*. Thus, midges grazed *Cocconeis*. However, the high α values for non-*Cocconeis* diatoms in midges indicate that midges preferentially grazed, or more easily consumed, these nonadnate diatoms (Steinman 1991, Dudley 1992), a possible indication of selective grazing (Hart 1985). Guts of midges from plates with Y *Cladophora* had even higher *Cladophora* content than guts of midges from plates with G *Cladophora*, a result suggesting that midges ingested *Cladophora* while attempting to graze adnate, tightly adhering *Cocconeis* cells. Lower *Cocconeis* densities on retreat-associated than on ambient filaments in Y *Cladophora* indicate a strong local effect of grazing.

R Cladophora.—Like in other studies (Steinman 1991, Dudley 1992), midges preferentially grazed on non-*Cocconeis* taxa, especially N-rich Rhopalodiaceae taxa. The higher densities of *Cocconeis* cells on retreat-associated filaments probably occurred because removal of the overstory of *Epithemia* during grazing exposed underlying epiphytes. Removal of overstory epiphytes can promote growth of understory algae (Dudley 1992), so the exposure of underlying *Cocconeis* cells may have increased their viability and promoted growth of associated *Chamaesiphon* (Stevenson and Stoermer 1982). Over longer time intervals in the river, midges remove epiphytes from R *Cladophora* and expose underlying filaments to yield macroscopically visible greening of *Cladophora* near midge retreats (see fig. 6 in Power et al. 2009). In our laboratory experiment, we did not observe macroscopic change in *Cladophora* color, but SEM micrographs of retreat-associated *Cladophora* filaments (Fig. 2E) and microscopic observations support field observations of epiphyte removal by midges. Ultimately, the color of the assemblage will depend on grazing rates relative to the growth rates of Rhopalodiaceae and of the *Cladophora* host.

Algal effects on midges.—Midge survival and the quality of midge retreats (length and density) were poor in plates with G *Cladophora* but better in plates with Y and R *Cladophora*. In the field, retreat-weaving midges are more common in Y and R stages of *Cladophora* and are rare in G *Cladophora* (Power et al. 2009). In our study, the low % cover of epiphytes and low density of branching in G *Cladophora* (Bergey et al. 1995) may not have provided sufficient roughness or structure for midges to grasp filaments, making it more difficult to build high-quality retreats. Poorer-quality retreats in G *Cladophora* would increase midge vulnerability to predators, such as the hydrophilid beetle larvae, *Enochrus* sp., which is common in *Cladophora* mats (Power 1990b). In contrast, the denser retreats built in Y and R *Cladophora* may protect midges from predation (Peckarsky 1982) and desiccation (Zamora-Munoz and Svensson 1996) in floating mats or as flow recedes and midge retreats are exposed to air. In Y and

TABLE 3. Densities of *Chamaesiphon* (cells/cm^2) on filaments of yellow and rusty-red *Cladophora* stages. Densities of *Chamaesiphon* were higher on yellow retreat-associated *Cladophora* than on after-midge ambient *Cladophora* filaments (ANOVA, $F_{3,34} = 3.389$, $p < 0.05$; Tukey post hoc: $p = 0.018$). No statistics were run on *Chamaesiphon* on rusty-red *Cladophora*.

Cladophora	Treatment	*Chamaesiphon*/cm^2
Yellow	Before	62,100 ± 28,133
	After-control	51,570 ± 10,696
	After-midge	13,365 ± 5282
	Retreat-associated	120,516 ± 18,118
Rusty-red	Before	0 ± 0
	After-control	0 ± 0
	After-midge	0 ± 0
	Retreat-associated	10,125 ± 4036

R *Cladophora*, midges appeared to tighten the weave of the filaments along the length of their retreats before pupation by weaving more *Cladophora* into the retreat or tightening the weave of filaments already present. Older midge retreats also are wider than new retreats (Power 1991). Caddisflies with stronger or wider cases are better protected from predators than caddisflies with weaker or narrower cases (Nislow and Molles 1993, Otto and Johansson 1995).

Food quality (i.e., polyunsaturated fatty acid and lipid content, C:N ratio) strongly affects growth rates and other fitness correlates of freshwater invertebrate primary consumers (Gresens 1997, Ravet and Brett 2006, Brett et al. 2009). *Pseudochironomus* larvae have higher specific growth and developmental rates and larger pupae when reared on a diet of diatoms than when reared on a diet of detritus (Gresens 1997). Food quality may increase over the course of epiphyte succession on *Cladophora* for 2 reasons. First, late-successional Rhopalodiaceae fix N, a limiting nutrient in the Eel River ecosystem (Hill and Knight 1988, Power 1991), so these unique diatoms are rich in proteins relative to other algae (Kupferberg 1994). Second, midges may spend less time and energy acquiring food as loosely attached epiphytes become relatively more abundant than adnate diatoms like *Cocconeis*. Therefore, we predict that as midges increase their consumption of diatoms and decrease their ingestion of low-quality *Cladophora* filaments during algal succession, midge growth rates should increase and their time to maturation should decrease. This prediction is supported by areal rates of emergence of adult midges, which are up to 25× greater from R than from G *Cladophora* mats (Power et al. 2009).

Indirect midge–algae interactions

Indirect midge-driven changes to epiphyte composition and % cover and to *Cladophora* health and growth (e.g., from nutrient inputs from excretion) could affect *Cladophora* microenvironments. For example, midges had a positive indirect effect on *Cocconeis* densities and reproduction in Y *Cladophora,* probably via nutrients from midge excretion. Midges may be increasing their food base by increasing densities of diatoms with fertilization (gardening sensu Ings et al. 2010) or by

TABLE 4. Mean relative biovolume units (%) of all algae (live and dead) and relative biovolume units of live vs dead cells from the foreguts and hindguts of midges from green, yellow, and rusty-red *Cladophora* stages. Cells were considered dead if they were completely void of cell contents. Cyano = cyanobacteria, Chl = Chlorophyta, F = N fixer, X = non-N-fixer. See Table 1 for taxon groupings.

			Green		Yellow		Rusty-red	
Division	F/X	Taxonomic grouping	Foregut	Hindgut	Foregut	Hindgut	Foregut	Hindgut
Diatoms	F	Rhopalodiaceae	22.6	18.2	14.0	17.2	93.6	94.6
Diatoms	X	*Cocconeis*	30.3	29.9	60.2	61.1	1.4	0.4
Diatoms	X	*Rhoicosphenia*	15.3	27.9	1.0	2.1	1.6	2.6
Diatoms	X	Other diatoms	18.9	9.1	0.2	0.4	2.7	0.7
Cyano	X	Non-N-fixing cyanobacteria	–	0.5	–	–	–	–
Chl	X	*Cladophora*	7.8	11.3	24.0	18.0	0.3	1.8
Chl	X	Chlorophyta	5.2	3.1	0.6	1.2	0.4	–
		Live cells	74.9	27.1	69.8	15.2	79.7	18.3
		Dead cells	25.1	72.9	30.2	84.8	20.3	81.7

TABLE 5. Average α_i values from the food preference model (Chesson1983; Case 1) based on algae found in midge foreguts and hindguts after grazing on green, yellow, and rusty-red *Cladophora* filaments and associated epiphytes. The model assumes food densities did not change (i.e., algal reproduction or consumption was insignificant compared to total amount of algal biomass available). α_i indicates a preference of the midge for particular algal taxon relative to the algal taxa available to graze. If $\alpha_i = 1$, then the midge diet consisted entirely of that food type. If $\alpha_i = 0$, then that food type was not present in the midge diet. Chl = Chlorophyta (*Cladophora* and other green filaments), Cyano = cyanobacteria, *E.* = *Epithemia*; *Rhoic* = *Rhoicosphenia*; *Cocc* = *Cocconeis*; other diatoms I = all other diatoms (*Nitzschia*, *Navicula*, *Gomphonema*, *Melosira*, etc.); other diatoms II = all diatoms excluding *Cocconeis*. For green and yellow *Cladophora* stages, diatoms were grouped into other diatoms II because of patchiness on the filaments and to provide sufficient data to run the model.

	By algal division			With diatoms in more detail						
Location/type of *Cladophora*	Diatoms	Chl	Cyano	*E. turgida*	*E. sorex/ E. adnata/ Rhopalodia*	*Rhoic*	*Cocc*	Other diatoms I	Other diatoms II	Chl	Cyano
Foregut											
Green	0.995	0.005	0.000				0.602		0.396	0.002	0.000
Yellow	0.894	0.106	0.000				0.301		0.627	0.089	0.000
Rusty-red	0.999	0.001	0.000	0.445	0.097	0.024	0.037	0.397		0.000	0.000
Hindgut											
Green	0.992	0.008	0.000				0.694		0.303	0.003	0.000
Yellow	0.910	0.090	0.000				0.165		0.817	0.018	0.000
Rusty-red	0.948	0.004	0.048	0.393	0.201	0.065	0.003	0.335		0.000	0.014

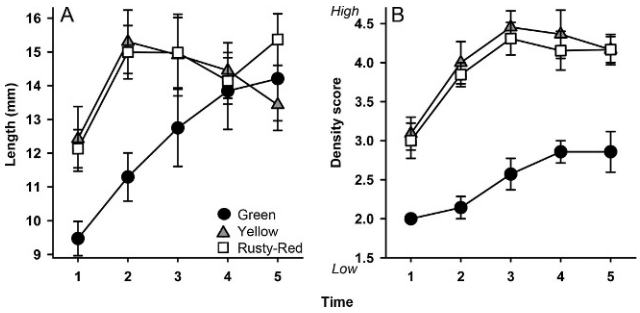

FIG. 4. Mean (±1 SE) retreat length (A) and density (B) for retreats built with green, yellow, and rusty-red *Cladophora* filaments. Time on the x-axis is presented sequentially and represents measurements taken every 8 to 12 h.

clearing epiphytes from *Cladophora* and increasing surface area for colonization by new food epiphytes (gardening sensu Hart 1985).

Midges had a positive indirect (nutrient-mediated) local effect on densities of cyanobacteria on retreat-associated filaments in both Y and R *Cladophora* stages. Algae, especially cyanobacteria and other small taxa with their high surface area to volume ratio (i.e., *Chamaesiphon* and *Calothrix*), may take advantage of local nutrient increases caused by midge excretion or feces (Liess and Hagland 2007), especially at the ends of midge retreats, or from nutrients released by cell breakage during grazing (Saba et al. 2011) and filament fragmentation during retreat construction. In Y *Cladophora*, *Chamaesiphon* at retreat ends and along ambient filaments may take advantage of leakage of nutrients, such as P, caused by *Cocconeis*-induced injury to *Cladophora* cell walls (Stevenson and Stoermer 1982). C*hamaesiphon*, like *Cocconeis*, exhibits luxury uptake of P (Stevenson and Stoermer 1982). Midge feces that accumulated in larval retreats were removed and deposited at retreat ends by midges, especially before pupation (PCF and AMC-C, personal observation). Fecal deposits can concentrate nutrients for uptake by algae. Pringle (1985) observed increases of diatoms on chironomid cases that probably were caused by nutrients excreted by larvae. In contrast, Bergey and Resh (1994) did not find an algal (chlorophyll *a*) response to fecal material from *Gumaga* (caddisfly) larvae.

When midges build retreats, they fragment *Cladophora* and cause turfs to detach (Power 1990a), thereby reducing local biomass. However, on smaller scales and during later phases of succession, midges may prolong viability (and possibly stimulate growth) of filaments in or near retreats, particularly detached *Cladophora*, by removing epiphytes (Dudley 1992) and regenerating nutrients. Midges often infest *Cladophora* proliferations in the Eel River at high densities

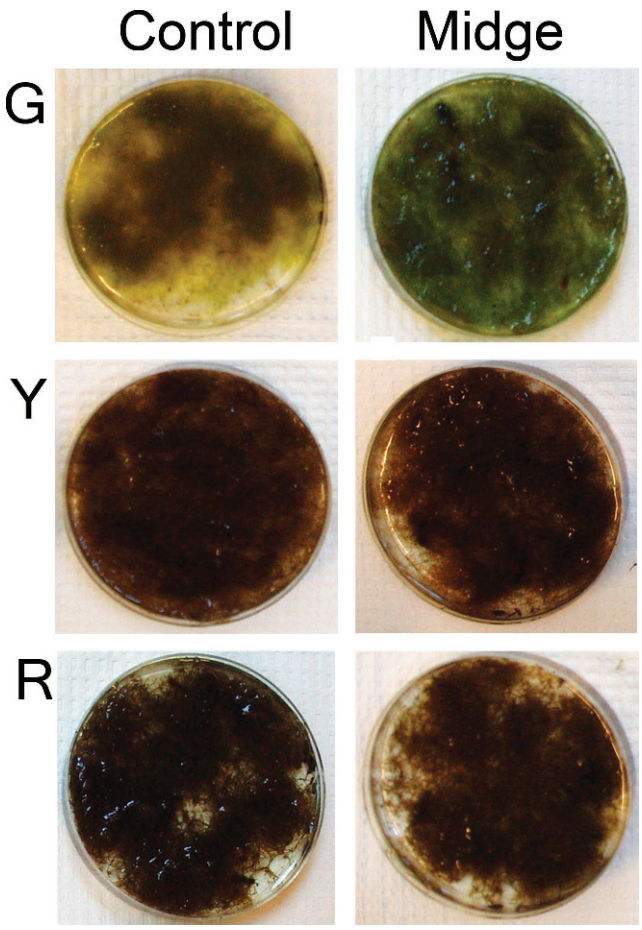

FIG. 5. Photographs taken of green (G), yellow (Y), and rusty-red (R) *Cladophora* grown with (midge) and without (control) midges at the end of the experiment. Note the degree of discoloration (decrease in health) in G *Cladophora* in the absence vs presence of midges.

(peaking seasonally at 40,000–60,000 individuals/m^2 plan-view area projected to the water surface; Power et al. 2008). Following scouring floods, proliferations of *Cladophora* in the Eel River during the early summer can be massive (Power et al. 2008). During many such years, 80 to 90% of *Cladophora* biomass is woven into retreats by midges (Power 1991). Thus, interactions of *Cladophora*, its epiphytes, and resident midges are likely to have basin-wide ecological consequences for the riverine ecosystem. These consequences also may ramify to watershed and nearshore marine ecosystems linked to the river by aerial exchange (N fixation; insect emergence) and downstream discharge of solutes, biomass, and detritus. Understanding ecology at markedly different scales (both temporally and spatially) should help us detect key watershed–river–ocean linkages, and predict ecosystem changes relevant to watershed and coastal management.

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