

EFFECTS OF WATER VELOCITY ON THE ARCHITECTURE AND EPIPHYTES OF *CLADOPHORA GLOMERATA* (CHLOROPHYTA)¹

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ABSTRACT

The architecture of the filamentous green alga *Cladophora glomerata* (L.) Kütz. and the composition of this alga's epiphytes [primarily the diatoms *Epithemia turgida* (Ehrenb.) Kütz., *Epithemia sorex* Kütz., and *Cocconeis pediculus* Ehrenb.] were examined in different velocity regimes. After transferring algal-bearing cobbles among velocities, the effects of changes in velocity were also examined. *Cladophora* branching pattern did not initially differ among slow, medium, and fast velocities, indicating that stable water velocities did not affect branching pattern. Two weeks after cobble transfer, *Cladophora* in fast velocity had fragmented more (i.e. had fewer filaments and fewer branch points per length of filament and had a higher percentage of unbranched filaments) than *Cladophora* in slow velocity. Fragmentation was greatest in tufts moved from slow velocity, suggesting velocity-associated differences in susceptibility to breakage. Epiphytic assemblage composition differed among slow, medium, and fast velocities and between locations on the filament (base and apex). *Cocconeis pediculus* dominated where exposure to high velocity was greater (filament apices in medium and fast velocities), whereas the *Epithemia* spp. dominated where lower velocities occurred (filament bases in all velocities and apices in slow velocity). Two weeks after the cobble transfer, the translocated diatom assemblages had changed and the original pattern of diatom distribution was restored.

Key index words: architecture; Bacillariophyceae; branching pattern; cyanobacterial endosymbionts; *Cladophora glomerata*; *Cocconeis pediculus*; *Epithemia*

Streams contain a mosaic of patches in which water velocity varies in space and time. On a coarse scale, spatial variation in velocity occurs, for example, between riffles and pools, and temporal variation occurs between spring runoff from snow melt and summertime base flow. At a finer scale, velocities vary around the edges of stones and, because of turbulence, the velocity at a single point on the streambed fluctuates widely. Further, these patches are affected by their velocity histories. Past velocities affect local substratum particle size and can affect

recruitment of organisms (e.g. by influencing choice of insect oviposition sites or algal zoospore settlement patterns).

Mobile organisms often select a preferred velocity range within this mosaic (Statzner et al. 1988), but sessile organisms, once established, must contend with changes in the velocity regime that occur at their fixed location (Koehl 1984). In streams, most animals are mobile, and most macrophytes and macroalgae are sessile. Thus, many aquatic insects select a range of velocities and move as velocities change (Statzner et al. 1988), but an attached macroalgal species cannot move and consequently experiences different water velocities across attachment sites. Moreover, each individual experiences local velocity changes, such as those associated with turbulence and spates.

Algal size and location determine, to a large extent, the degree to which organisms experience velocity changes. Small forms, such as the diatom *Achnanthes*, are usually less affected (Peterson and Stevenson 1990, 1992). Surface irregularities may be protective, as has been shown for the basal rhizoidal cells of the green macroalga *Cladophora* (Dudley and D'Antonio 1991). Larger forms, such as filamentous tufts of *Cladophora* or large branched colonies of the diatom *Gomphonema*, extend into the current and are subjected to the force exerted by moving water and abrasion from suspended materials (Vogel 1981). Epiphytic algae, which are generally small, may be exposed to the full force of the current if they occur on the outer edges of the host plant.

Comparison between riffle and pool sections of streams (Korte and Blinn 1983, Oemke and Burton 1986) provides insight into how water velocity affects algal communities. Nutrient levels, temperature, and light level can be matched between riffles and pools, whereas velocity will differ. The faster velocity in riffles may affect the architecture or cell wall characteristics of filamentous macroalgae, and the density or taxonomic composition of its epiphytes, relative to conditions found in algal communities in the slower velocity of pools. Changes may be in response to physical forces of the current, to direct damage to filaments or removal of individuals, or to indirect effects, such as grazing by herbivores.

Cladophora glomerata (L.) Kütz. is a widely occur-

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ring branched macroalga (Blum 1956, Sheath and Cole 1992) that often supports a dense growth of epiphytes (Whitton 1970, Lowe et al. 1982, Dodds and Gudder 1992). Studies have shown a trend of increased branching in *Cladophora* with increased water velocity (van den Hoek 1964, Parodi and Cáceres 1991). These studies describe natural patterns in streams with unknown velocity histories and lack experimental manipulations. Epiphytes of *Cladophora* are typically described for entire filaments or tufts (e.g. Chudyba 1965, Stevenson and Stoermer 1982, Hardwick et al. 1992), without regard to their location on the filaments. Exceptions describe differences in epiphyte assemblages among differently aged portions of *Cladophora* filaments (Otten and Willemse 1988) and changes in assemblages along the length of filaments that are exposed or not exposed to wave action (Luttenton and Rada 1986). As is the case for *Cladophora* branching, studies of *Cladophora* epiphyte distribution are strictly observational.

In this study, we examined the architecture of *Cladophora glomerata* and the distribution of its algal epiphytes in relation to water velocity in a stream with a long period of stable discharge (thereby minimizing any effects of velocity history). We then assessed the effect of a changed velocity regime experimentally by transferring *Cladophora*-bearing cobbles among velocities and examining changes in *Cladophora* and its epiphytic assemblages. Thus, we were able to differentiate the effects of stable and of changed water velocities. We also tested the suggestion that algae from low-stress habitats will be more affected by high water velocity than algae from high-stress environments (Steinman and McIntire 1990).

MATERIALS AND METHODS

The South Fork of the Eel River (Mendocino County, California) is a third-order stream as it flows through the University of California's Northern California Coast Range Preserve (latitude 30°44', longitude 123°38'). Cobble and boulder dominate much of the streambed, even within pools. The stream is typically shaded by surrounding hillsides and trees (primarily Douglas fir, *Pseudotsuga menziesii* Franco). However, the study site is next to a dry, abandoned streambed and receives direct sun for 6–7 h daily. Because the area has a Mediterranean climate (winter rain, dry summers), the stream's discharge changed little and remained at base flow during the study (12–27 June 1991).

Cladophora glomerata is abundant in the Eel River, where it may grow extensively and forms floating mats during the summer (Power 1990a, 1992). Growth from overwintering rhizoidal cells begins in early spring, after the end of winter rains (Power 1992). Rapid growth produces long tufts in late spring and early summer. Because long tufts are morphologically complex, have variable flow conditions within them (Dodds 1991b), and may be more liable to breakage (Entwisle 1989), short tufts (most less than 3 cm long) occurring soon after *Cladophora* growth began were studied.

Three sites with non-overlapping velocity regimes were selected within a 50-m run-riffle sequence. Sites had similar light regimes and water depths. The upstream site was located at the tail of a pool and had a sand-gravel-cobble substratum and a

velocity of approximately $0.015 \text{ m}\cdot\text{s}^{-1}$ (= slow velocity). Slow velocities were estimated by timing a floating twig because they were below the detection limits of the Teledyne Gurley Pygmy Current Meter used at the other sites. The middle site had a cobble-boulder substratum and a water velocity of $0.16\text{--}0.27 \text{ m}\cdot\text{s}^{-1}$ (= medium velocity), and the lower site was located in the downstream riffle and had a cobble-boulder substratum and water velocity of $0.40\text{--}0.93 \text{ m}\cdot\text{s}^{-1}$ (= fast velocity). Velocity ranges were calculated from 12 velocity measurements per site on 12, 13, and 27 June.

Cladophora tufts (and their associated epiphytes) were collected from 12 cobbles within each velocity regime on 12 June 1991. Cobbles were lifted out of the water and, using fine forceps, 8–12 *Cladophora* tufts were randomly selected and removed. Tufts were placed in labeled vials containing 6% formalin, and the cobbles, from which only a small percentage of the tufts had been removed, were returned to the stream.

To assess the influence of changes in velocity, we transferred these same cobbles among the three velocity regimes on 13 June 1991. An area of approximately 1 m^2 within each velocity regime was cleared of cobbles. The 36 cobbles used in the initial survey were then placed in the cleared areas using a stratified random design, so that the 12 original cobbles from each velocity site were distributed with four at each site (including the site from which the cobbles were originally taken). *Cladophora* tufts were harvested after 2 weeks (on 27 June), using the same techniques as those used before cobble transfer.

For both the initial survey and the transfer experiment, three tufts from each cobble were randomly selected for analysis of *Cladophora* architecture, and data from the three tufts were later pooled and treated as a single replicate (i.e. $n = 12$ per velocity regime, or $n = 4$ per initial-final velocity combination). Individual filaments emerging from the basal attachment were separated and counted. Five of these filaments per tuft were randomly selected, individually mounted on slides, and traced onto paper using a Ken-o-vision Microprojector (Model X-1000-1; magnification = $6.5\times$). Drawings were used to measure filament length and to count the number of branch points (counted at the location of branching and calculated as number per millimeter of filament length) and the number of unbranched filaments.

Two tufts from each cobble were used to count algal epiphytes. Water mounts of two filaments per tuft were examined at $400\times$ magnification and *in situ* algal counts were made along three contiguous lengths of a Whipple micrometer (total measured distance = 0.55 mm). Counts were made both at the apex of the filament and near the base (just above the first branch point). The three numerically dominant diatom species [*Epithemia turgida* (Ehrenb.) Kütz., *Epithemia sorex* Kütz., and *Cocconeis pediculus* Ehrenb.] were counted separately, but other diatom taxa were generally combined (because they were much less common and often obscured by the dominants). In the initial survey, the filamentous blue-green alga *Calothrix* sp. (Cyanophyta) was also counted; this taxon was not counted after cobble transfer because it was hard to see when diatom density was higher. Counts were converted to number of cells per millimeter of filament and combined to produce one base and one apex replicate per cobble ($n = 12$). Because of the *in situ* counting technique, only the epiphytes on the upper surface of the *Cladophora* filaments in the wet mounts could be counted; therefore, counts are underestimates of epiphyte numbers but provide data that are comparable within this study.

Additionally, the number of cyanobacterial endosymbionts per cell of *E. turgida* was determined in the initial survey by counting endosymbionts in 12 *E. turgida* on the base and apex of each filament examined. Endosymbionts appeared as spheres resting beneath the frustule of *E. turgida*. Although *E. sorex* also contains endosymbionts, they were not counted because endosymbiont number was low (only one or two per cell).

Prior to statistical analysis, most data were normalized by trans-

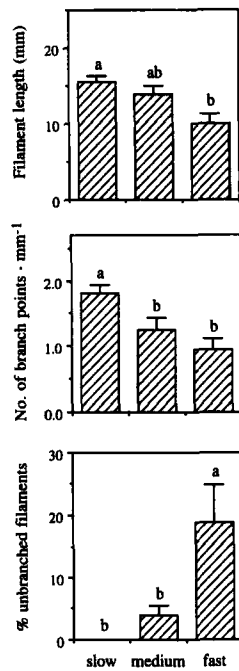


FIG. 1. Means (\pm SE) for *Cladophora* branching pattern characters 2 weeks after cobble transfer among velocities. Velocities (slow, medium, and fast) are velocities after cobble transfer. Significantly different (Tukey's test or Bonferroni's inequality; $P \leq 0.05$) means are indicated by different letters above the bars.

formation using $\log(x + 1)$. One data set (the percentage of unbranched *Cladophora* filaments) was not normally distributed, even with arcsin square root transformation, and was analyzed nonparametrically. ANOVA tests were run on transformed data. The P values used to determine significance were adjusted in cases where several ANOVAs were run on similar data [i.e. the four measures of branching in *Cladophora* and densities of the three (after cobble transfer) or four (before cobble transfer) epiphytic taxa]. In these data sets, the P values used were 0.017 ($=0.05/3$) or 0.012 ($=0.05/4$).

Measures of *Cladophora* branching pattern were analyzed with one-way ANOVA (independent variable = initial velocity, $n = 12$ per cell) before cobble transfer and two-way ANOVA (independent variables = initial velocity and final velocity, $n = 4$ per cell) after cobble transfer. The percentage of unbranched filaments was analyzed by the Kruskal-Wallis test before cobble transfer and Friedman's test after cobble transfer. Epiphyte density was analyzed with two-way ANOVA (independent variables = initial velocity and location on the filament, $n = 12$ per cell) before cobble transfer and three-way ANOVA (independent variables = initial velocity, final velocity, and location on the filament; $n = 4$ per cell) after cobble transfer. Tukey's multiple comparison test, corrected for significant interaction effects where appropriate, was used to distinguish significantly different treatments following ANOVA tests, and Bonferroni's inequality was used following Friedman's test.

RESULTS

At base flow in the South Fork of the Eel River, the architecture of *Cladophora* did not differ significantly among slow, medium, and fast water velocities (one-way ANOVA for number of filaments, filament length, and density of branch points; Kruskal-Wallis test for percentage of unbranched filaments).

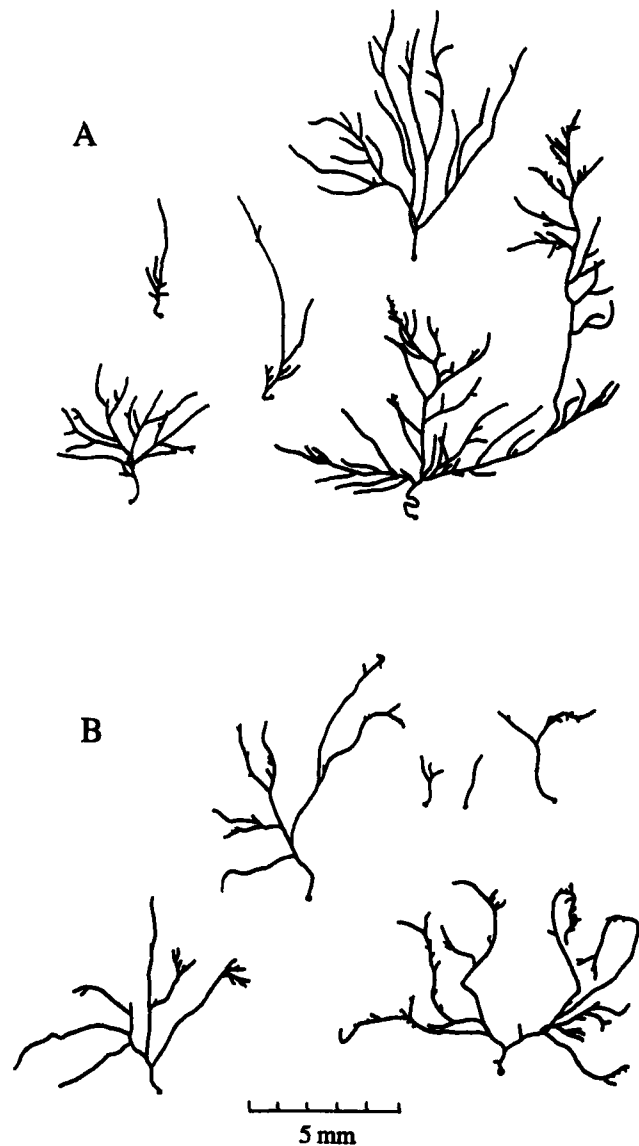


FIG. 2. Example of tracings of projected filaments from *Cladophora* tufts showing the velocity combination of initial slow-final fast. A) Filaments from a single tuft collected in slow velocity on 12 June. B) Filaments from a tuft collected from the same cobble as A, which had been transferred to fast velocity 2 weeks before sampling on 27 June.

The range of character means among velocities for young *Cladophora* tufts was 24–32 filaments emerging from the basal holdfast ($F = 1.92$, $P = 0.16$), with a filament length of 10–20 mm ($F = 2.7$, $P = 0.08$), 1.7–1.9 branch points per millimeter of filament ($F = 0.1$, $P = 0.88$), and fewer than 1% unbranched filaments ($H = 1.36$, $P > 0.10$).

Cladophora tufts on transferred cobbles differed significantly among final velocity regimes for three of the four measured characters [mean filament length, number of branch points per millimeter of filament (two-way ANOVA; Table 1, Fig. 1) and the percentage of unbranched filaments (Friedman's test, initial velocity: $\chi^2 = 1.63$, $P > 0.25$; final velocity: $\chi^2 = 13.34$, $P < 0.005$)]. Fast velocity produced tufts

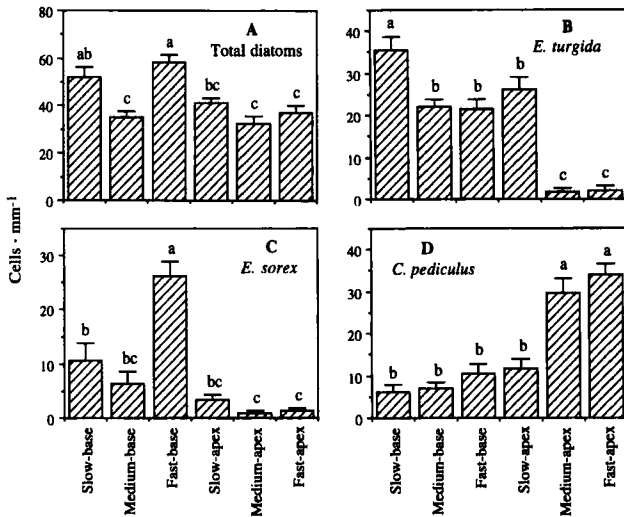


FIG. 3. Distribution of epiphytic diatoms on *Cladophora* filaments in the initial survey on 12 June. Means (\pm SE) are shown for combinations of velocity (slow, medium, and fast) and location on the filament (base and apex). A) All diatoms (= Total). B–D) Each of the dominant species. Significantly different (Tukey's test; $P \leq 0.05$) means are indicated by different letters above the bars.

where *E. turgida* and *E. sorex* were least dense (e.g. at the apices in medium and fast final velocities; Fig. 5G cf. A and D). Initial velocity also had an effect (Fig. 5F); *Cladophora* tufts initially located in medium and fast velocities supported more *C. pediculus* than tufts initially located in slow velocity.

A continuing effect of initial occurrence at slower velocities was supported by significant interactions between initial and final velocities for *E. turgida* and *C. pediculus* (Table 3). Tufts initially from slow velocity (for *C. pediculus*) or slow and medium velocities (for *E. turgida*) that remained in or were transferred to slow velocity had significantly fewer *C. pediculus* and significantly more *E. turgida* than other velocity combinations.

Distribution patterns were also evident for other diatom species. The large upright diatom *Rhoicosphenia curvata* (Kütz.) Grun. ex Rabh. and branched colonies of *Gomphonema olivaceum* (Lyngb.) Kütz. were found almost exclusively on filament apices in

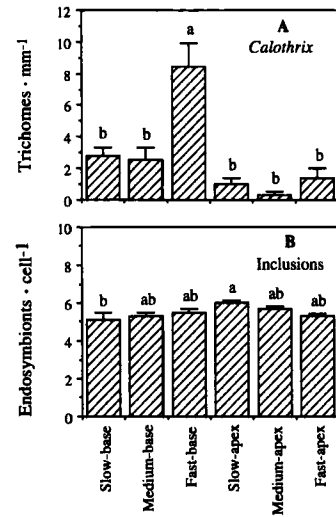


FIG. 4. Distributions on *Cladophora* filaments of A) the blue-green alga *Calothrix* and B) cyanobacterial endosymbionts in *Ephithemia turgida* cells in the initial survey on 12 June. Means (\pm SE) are shown for combinations of velocity (slow, medium, and fast) and location on the filament (base and apex), and significantly different (Tukey's test; $P \leq 0.05$) means are indicated by different letters above the bars.

slow velocity (mean density = 40.3 cells · mm⁻¹ of filament). At all other location-velocity combinations, the small upright diatom *Achnanthes* spp. was abundant (mean density = 16.7–22.9 cells · mm⁻¹, except for filament bases in slow water where the lower density of 5.9 cells · mm⁻¹ may have resulted from visual obstruction from the high *E. turgida* density).

DISCUSSION

The architecture of young *Cladophora* tufts may be more influenced by changes in water velocity than by an unchanging velocity regime. In the Eel River during the summer dry season, *Cladophora* growing in a relatively unchanging low discharge was morphologically unaffected by the local velocity regime, whether the velocity was fast, medium, or slow. In contrast, major architectural differences resulted after a change in velocity, especially after a velocity increase. In our experiment, this change

TABLE 3. Results of three-way ANOVAs examining the effects of initial velocity (slow, medium, and fast; before stone relocation), final velocity (after stone relocation), and location on *Cladophora* filaments (base and apex) on three common epiphytic diatoms. Significant P values ($P \leq 0.017$) are indicated by asterisks.

| Source | df | <i>E. turgida</i> | | <i>E. sorex</i> | | <i>C. pediculus</i> | |
|-----------------------|----|-------------------|----------|-----------------|----------|---------------------|----------|
| | | F | P | F | P | F | P |
| Initial velocity (=A) | 2 | 0.69 | 0.507 | 8.54 | 0.0006* | 7.74 | 0.001* |
| Final velocity (=B) | 2 | 100.93 | <0.0001* | 20.47 | <0.0001* | 126.76 | <0.0001* |
| Interaction AB | 4 | 4.18 | 0.005* | 0.56 | 0.695 | 3.67 | 0.010* |
| Location (=C) | 1 | 132.50 | <0.0001* | 26.39 | <0.0001* | 75.00 | <0.0001* |
| Interaction AC | 2 | 1.29 | 0.283 | 0.70 | 0.503 | 0.06 | 0.939 |
| Interaction BC | 2 | 13.42 | <0.0001* | 1.00 | 0.375 | 5.21 | 0.009* |
| Interaction ABC | 4 | 2.55 | 0.050 | 1.24 | 0.303 | 3.23 | 0.019 |
| Error | 54 | | | | | | |

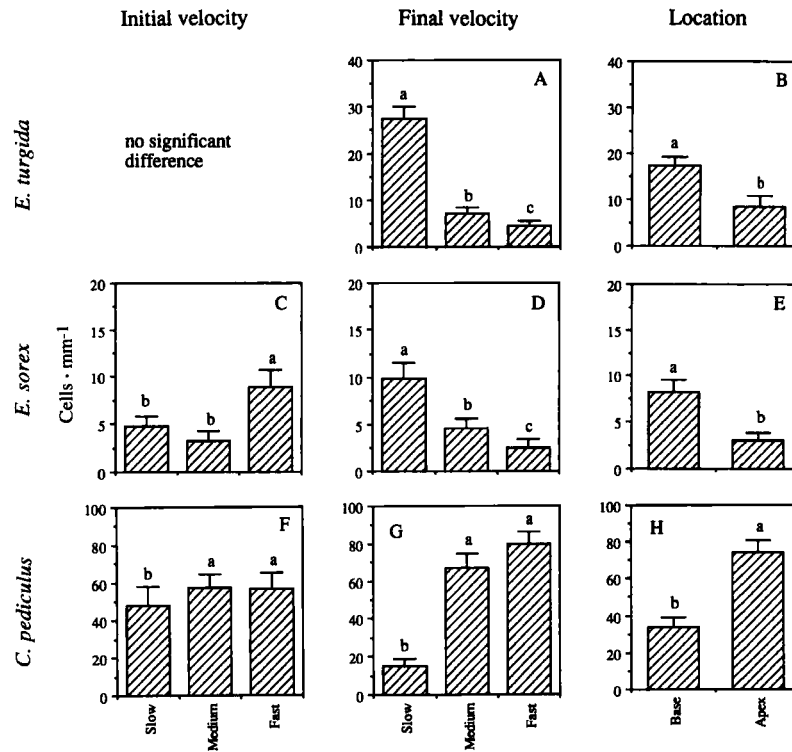


FIG. 5. Distribution of epiphytic diatoms on *Cladophora* filaments 2 weeks after cobbles were transferred among velocities. Density means (\pm SE) are shown for initial velocity (= velocity before cobble transfer; slow, medium, and fast), final velocity (= velocity after cobble transfer; slow, medium, and fast) and location on the filament (base and apex) for each of the three dominant taxa.

was accomplished by transferring cobbles among velocity regimes; in streams where the climate lacks a dry season, increased velocity changes occur during spates.

Fragmentation within tufts was more prevalent than growth during the study, as shown by decreases in mean filament length and the number of branch points per millimeter over time. *Cladophora* tufts on the transferred cobbles did not appear different from surrounding *Cladophora*, indicating that this lack of growth occurred generally in the stream. Indeed, *Cladophora* growth was not luxuriant and floating mats did not form during the summer of 1991 (compared to other years; e.g. Power 1990a, 1992).

Most fragmentation of *Cladophora* tufts occurred when velocity was greatly increased (i.e. from slow to fast velocity), a situation similar to that found in stream pools during subscouring spates. Based on this result, we would expect a greater loss of *Cladophora* from pools than riffles during subscouring spates (per the prediction of Steinman and McIntire 1990), because pools experience relatively greater increases in velocity than riffles (Keller 1971). During scouring spates, macroalgae would be lost from both habitats and, indeed, Power and Stewart (1987) found that macroalgae in pools and riffles were equally susceptible to dislodgment.

Our finding of the similarity in *Cladophora* architecture across water velocities does not conform directly with the results of previous studies. Both van

den Hoek (1964) and Parodi and Cáceres (1991) have described a relationship of more branching with higher velocity. In streams without a stable velocity (such as the ones they studied), frequent spates that cause greater fragmentation of *Cladophora* in slow velocity sites than in fast velocity sites would also result in an overall pattern of more branching in fast velocity. Hence, it is unclear whether the pattern of increased branching with increased water velocity results from increased branching or reduced fragmentation. We studied a phenologically young population (tufts were generally under 3 cm long); in an older population, differential sloughing of long streamers or mats (Entwistle 1989) would also result in architectural differences among velocity regimes.

Two factors that likely affect susceptibility to fragmentation by increased velocity are characteristics of the cell wall and epiphyte load. Increases in cell wall thickness or changes in wall composition may occur with faster velocity (Raven 1992); this may result, in turn, in filaments that withstand fragmentation, especially if filament flexibility is enhanced (Vogel 1981). Epiphytes may increase drag and fragmentation (Dudley 1992), although measurements have shown reduced drag (Dodds 1991a). High epiphyte density may also affect cell walls and produce brittle filaments (Chudyba 1965, Dudley 1992, C. Boettiger, pers. observ.). Epiphytes colonize slower in fast velocity than in slow velocity (Steinman and

McIntire 1986, Peterson and Stevenson 1989) and are more readily removed if poorly attached (Peterson and Stevenson 1990, 1992) in fast velocity. *Cladophora* tufts in slow velocity tend to have more epiphytes and/or higher profile epiphytes (e.g. Luttenton and Rada 1986, Otten and Willemse 1988, this study) and are thus more affected by damage to cell walls and possibly drag. They should fragment more easily when velocity is increased.

The observed pattern of epiphyte distribution on *Cladophora* filaments was similar before and after cobble transfer and is best explained by differential susceptibility of the dominant diatoms to dislodgment by fast velocity. The low-profile *C. pediculus* dominated filament apices in medium and fast velocities, locations where it was exposed to fast-flowing water. Consequently, *Cladophora* tufts in fast velocity were bright green. Conversely, the higher profile *E. turgida* and *E. sorex* dominated on filament bases at all velocities and on filament apices only in slow velocity, locations where velocities are relatively slower (e.g. Dodds 1991a). *Cladophora* tufts in slow water were brownish, and the filaments appeared thicker because of the encrusting epiphytes. In areas exposed to wave action on the Mississippi River, Luttenton and Rada (1986) found a similar transition of epiphytes along *Cladophora* filaments: *C. pediculus* was sparse on apices, abundant on mid-filaments, and intermixed with higher profile diatoms near the bases. Otten and Willemse (1988) also noted that taller epiphytes of *Cladophora* were more easily removed by current than low-profile epiphytes.

Three mechanisms (other than direct effects of water velocity) for the observed within-filament pattern of epiphyte distribution include diatom colonization patterns, nutrient limitation, and grazing. Rapid colonization and dominance of growing apices by *C. pediculus* is an improbable mechanism because growth in *Cladophora* occurs both within filaments and at apices (Whitton 1970), and early colonizing diatoms tend to be large forms (Steinman and McIntire 1986, Tuchman and Stevenson 1991) rather than small forms such as *C. pediculus*. Additionally, *C. pediculus* was abundant on both young and frayed (old or former zoospore-producing) apices.

The second mechanism is that nutrients are more limiting at the base of tufts and in slow velocity because of reduced water flow in these areas and, as a consequence, *E. turgida* and *E. sorex* dominate in these locations. Both *Calothrix* (Stewart 1973) and the endosymbionts in *Epithemia* (DeYoe et al. 1992) have been implicated in nitrogen fixation and may be useful as indicators of nitrogen limitation. Algae in the Eel River are nitrogen-limited (Power 1990b), which correlates with the high density of *Epithemia* spp. (Fairchild and Lowe 1984, Peterson and Grimm 1992). The lack of correspondence between the distributions of *Calothrix* and *E. turgida* (the two species

we used as indicators) and the similarity in number of endosymbionts across all velocity–location combinations indicate that locational differences in nitrogen limitation are either small or that entire *Cladophora* tufts were severely nitrogen-limited and our indicators could not distinguish differences.

The third mechanism is that grazers produced the observed pattern and, indeed, grazers can affect epiphyte communities on *Cladophora* (Dodds 1991a, Dudley 1992). *Cocconeis* is a grazer-resistant taxon that can be abundant under high grazing pressure (Jacoby 1987, Lamberti et al. 1989, Dudley 1992). *Cocconeis pediculus* was most abundant in fast velocity at filament apices, a location where grazer density should be lower because of fast water velocity (Scott 1958, Poff and Ward 1992). Therefore, our data indicate that grazers did not produce the observed pattern.

Although the same epiphyte distribution pattern was evident before and after cobble transfer, densities of *E. sorex* and *C. pediculus* after transfer were somewhat affected by initial velocity. Densities of both taxa were higher on filaments initially from faster velocities, suggesting that, when transferred to slow velocity, *E. sorex* was able to establish in areas initially dominated by *C. pediculus* and that, when kept in faster velocities, *C. pediculus* maintained dominance. After tufts were transferred, *E. turgida* colonized all initial velocities equally and resisted invasion by other diatoms, suggesting that *E. turgida* was the strongest colonizer of the three dominant diatom species.

The difference in turnover time between *Cladophora* and its diatom epiphytes resulted in differing effects of changed water velocity. Because of *Cladophora*'s longer turnover time (generally a year or longer; Whitton 1970, Entwisle 1989, Power 1992), the sampled tufts had experienced velocity changes and architectural differences were evident, especially by fragmentation associated with increased velocity. The shorter turnover time of diatoms (at most, a few days because of immigration and rapid cell division; e.g. Oemke and Burton 1986) meant that, during the sampling interval, diatoms passed through several cycles of division and new colonizers had probably established. The general pattern of diatom distribution had returned to the original pattern by the second sampling date, demonstrating nearly complete readjustment to changed velocities. Tracking both *Cladophora* and its epiphytes over a set of water velocity changes provided information at several spatial–temporal scales. Included are microscale differences (i.e. by the longitudinal distribution of diatoms on filaments), effects of past conditions (i.e. by differing fragmentation patterns of *Cladophora* from different habitats), and taxon-specific temporal responses to changing conditions (i.e. by fragmentation in *Cladophora* and species replacement among epiphytic diatoms).

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