PRIMARY RESEARCH PAPER

# Macroinvertebrate colonization dynamics on artificial substrates along an algal resource gradient

**A. Braccia · S. L. Eggert · N. King**

**Abstract** Riparian canopy removal and land use may introduce multiple stressors that can alter food and habitat for stream organisms, but the influence of these alterations on macroinvertebrate colonization dynamics is less well known. A field study involving the simultaneous placement and removal of artificial substrates was performed to examine how macroinvertebrate colonization rates might vary with algal accumulation within a perennial stream segment in eastern Ohio, USA. The study was conducted over a 60-day summer colonization period in three reaches that were selected to represent an algal resource gradient according to canopy cover and agricultural nutrient sources in the riparian corridor. Total nitrogen, water temperatures, and mean algal biomass from substrates increased along the resource gradient represented by the study sites. Total macroinvertebrate biomass and the abundance and biomass of scrapers also increased according to the gradient. Correlation results indicated that chlorophyll *a* biomass, rather than time or temperature, was better related to the abundance and biomass of most primary consumers on substrates. These results suggest that the combined effects of elevated temperatures and nutrients can result in relatively rapid algal accrual that may alter the colonization and establishment of macroinvertebrate communities in streams subjected to gradients of riparian disturbances.

**Keywords** Functional feeding groups · Chlorophyll *a* · Periphyton · Nutrients · Agriculture · Riparian canopy

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## Introduction

Identifying factors that influence the colonization dynamics of stream macroinvertebrates can improve our understanding of stream recovery following natural and anthropogenic disturbance and help explain temporal variability in community structure that is commonly observed in benthic macroinvertebrate studies. Since the degree and extent of disturbance determines the size of habitat patches available for colonization, studies of macroinvertebrate colonization are conducted over large (e.g., rivers, streams; Williams & Hynes, 1977; Gray & Fisher, 1981; Minshall et al., 1983a; Malmqvist et al., 1991; Milner et al., 2000) and small (e.g., stones, patches; Wise &

Molles, 1979; Shaw & Minshall, 1980; Peckarsky, 1986; Robinson et al., 1990) spatial scales. The simultaneous placement and removal of artificial substrates is an approach that has been widely used to study macroinvertebrate colonization of benthic substrate patches following small-scale disturbance, such as flow-generated scour or tumbling of rocks (Ciborowski & Clifford, 1984; Lake & Doeg, 1985; Robinson & Minshall, 1986; Downes & Lake, 1991; Rutherford, 1995; Baer et al., 2001; Miyake et al., 2003).

The succession of taxa and trophic groups onto benthic habitats has been well described from macroinvertebrate colonization studies. In general, highly mobile, opportunistic taxa within the collector-filtering or -gathering functional groups will colonize first and then increases in the abundance of scrapers, predators, and shredders can occur (see review by Mackay, 1992). Colonization models predict that early dynamics are primarily a result of stochastic factors and that initial colonization should quickly increase to maximum abundance, biomass, or taxa richness, and then remain at an equilibrium level (Sheldon, 1984; Minshall & Petersen, 1985). Time to equilibrium (i.e., stabilization time) is often equated with plateaus (or maxima) in macroinvertebrate densities, biomass, or taxa richness. Results from small-scale colonization studies have shown that initial colonization is rapid (2–4 days), but individuals of different taxa and trophic groups colonize at different rates, and time to equilibrium in densities and richness is variable and generally ranges from 4 to 30 days (Rosenberg & Resh, 1982; Mackay, 1992). In some studies, equilibrium in total macroinvertebrate densities or richness on substrates was never reached and successional changes in individual taxa extended beyond stabilization times for total densities or richness (Meier et al., 1979; Peckarsky, 1986; Baer et al., 2001; Miyake et al., 2003).

Variation in stabilization times for macroinvertebrate densities has been attributed to season, experimental design, and the densities, mobility, and life histories of available colonists (Rosenberg & Resh, 1982; Robinson et al., 1993; Miyake et al., 2003). Studies from temperate streams have demonstrated that colonization rates of macroinvertebrates are more rapid during summer and early fall when elevated stream temperatures increase macroinvertebrate activity and more recruits are present (Shaw & Minshall,

1980; Williams, 1980; Robinson et al., 1993; Matonickin et al., 2001). Simultaneous measures of basal food resources (e.g., algae and detritus) have not always been reported from colonization studies, so it is difficult to generalize about how the accumulation of these resources influence macroinvertebrate community colonization. However, continuous increases in macroinvertebrate densities and richness have been attributed to changes in habitat and the accumulation of food resources on substrates over colonization intervals (Meier et al., 1979; Shaw & Minshall, 1980; Baer et al., 2001), and more rapid colonization of substrates by macroinvertebrates has been reported from studies that used substrates with natural or artificial periphyton layers (Robinson et al., 1990; Baer et al., 2001; Miyake et al., 2003). Further, Robinson et al. (1990) suggested that variable stabilization times for macroinvertebrate densities from small-scale colonization studies may be partly explained by the presence of a periphyton layer. Since algal resources may provide food and habitat for certain macroinvertebrates, equilibrium is unlikely to develop if substrates are continuously accumulating epilithic material (Mackay, 1992).

Benthic food resources can be altered in stream reaches where native forest has been removed from riparian zones because increased solar radiation and temperatures can enhance standing stocks of periphyton and primary production (Lowe et al., 1986; Hill et al., 1995; Quinn et al., 1997; Kiffney et al., 2003). Riparian canopy removal also reduces forest litter inputs that support the detrital-based food webs of temperate streams, and results from field studies have shown that timber harvest from riparian zones can increase the abundance of macroinvertebrates and alter the functional composition of macroinvertebrate communities (Newbold et al., 1980; Hawkins et al., 1982; Wallace & Gurtz, 1986). In addition, agricultural land use within watersheds can introduce inorganic nutrients (Broussard & Turner, 2009; Hill et al., 2011) that may interact with light and elevated temperatures and further stimulate primary production. Altered riparian zones and nutrient inputs have been identified as major stressors to benthic macroinvertebrate communities (Dodds & Welch, 2000; Paulsen et al., 2008). Results from the analysis of large observational datasets have revealed that macroinvertebrate-based indicators of biological integrity (e.g., EPT taxa, total taxa richness) are negatively

correlated with nutrients in wadeable streams in some regions of the U.S. (Miltner & Rankin, 1998; Wang et al., 2007; Yuan, 2010). Understanding the relative role of algal resource accrual on macroinvertebrate colonization dynamics may reveal mechanisms that influence the structure of benthic macroinvertebrate communities in agricultural streams. We are unaware of any small-scale colonization studies that have addressed the question of how macroinvertebrate colonization of artificial substrates might be influenced by the combined effects of reduced riparian canopy cover and agricultural land use.

Since primary productivity can be enhanced by light, temperature and nutrients, and macroinvertebrate colonization dynamics can be influenced by algal accrual on substrates, we hypothesized that macroinvertebrate community colonization dynamics would vary within a stream segment according to canopy cover and agricultural nutrient sources within the riparian corridor. The objective of our study was to measure macroinvertebrate colonization rates on artificial substrates along an a priori selected gradient of stress (represented by three study sites) during a single season. Artificial substrates in this study served to mimic bare patches of benthic habitat that are created from flow-generated disturbance. We expected that algal resources would accumulate on substrates in all study sites, but that rates of algal accumulation would differ among sites according to available light, nutrients, and water temperature. In turn, we hypothesized that the total densities and biomass of macroinvertebrates, as well as certain taxa and trophic groups (e.g., scrapers), would increase with algal accumulation on substrates.

## Methods

### Study sites

The study sites were three, non-consecutive 100-m reaches in a segment of Silver Creek, Portage County, OH, USA. Silver Creek is a third order tributary within the upper Mahoning River watershed of the Ohio River basin (Fig. 1). The watershed is located within the Erie-Ontario Lake Plain ecoregion (Omernik, 1987), and substrates of the streambed are shale and sandstone mixed with sand and gravel from Mississippian and Pennsylvanian age lithographies. The

region receives an average of 96 cm of precipitation per year. Based on coverage from the 2006 National Land Cover Database (Homer et al., 2007), the watershed is predominantly forested (49%) with cultivated crops and pasture (41%) and low/medium intensity development (9%). Land use in the riparian corridor is variable and areas of agricultural and light residential use are interspersed among patches of continuous forest.

The "low" end of the expected resource gradient has a forested riparian zone (Forested Site) and is located at the Hiram College's James H. Barrow Field Station. The field station contains 200 acres of beech-maple forest and no agricultural nutrient sources. In 2006, the Forested Site was classified as Coldwater Habitat for fish and macroinvertebrates and fully supported its aquatic life use designation with an Invertebrate Community Index Score of 52 (Ohio Environmental Protection Agency, 2008). The other study sites that represented "medium" and "high" portions of the expected resource gradient have minimal canopy cover—dubbed open sites—and are located upstream (Open Site 1) and downstream (Open Site 2) of the Forested Site. Open Site 1 is 3.5 km upstream from the Forested Site and has riparian vegetation that consists of grasses and shrubs that are occasionally mowed by the land owner. Open Site 2 is 2 km downstream from the Forested Site and has similar riparian vegetation to Open Site 1. Land use immediately adjacent to the Forested Site and Open Site 1 did not change between 2006 and the time of this study (2009). However, trees within the riparian zone of Open Site 2 were removed during a timber harvest operation in the lower portion of the watershed in 2008.

No agricultural nutrient sources are adjacent to the riparian zones of the Forested Site and Open Site 1. The nearest nutrient sources are row crops at approximately 800 m upstream of Open Site 1 and 980 m upstream of the Forested Site, and stream segments immediately upstream of both sites have forested riparian zones. Open Site 2 receives drainage from row crop agriculture that is immediately upstream and adjacent to the riparian zone. Further, cattle have access to Silver Creek at approximately 700 m upstream of Open Site 2. We expected that the study sites—ordered Forested Site, Open Site 1, and Open Site 2—would represent an algal resource gradient as a result of potential stressors associated with riparian conditions and nutrient sources described above.
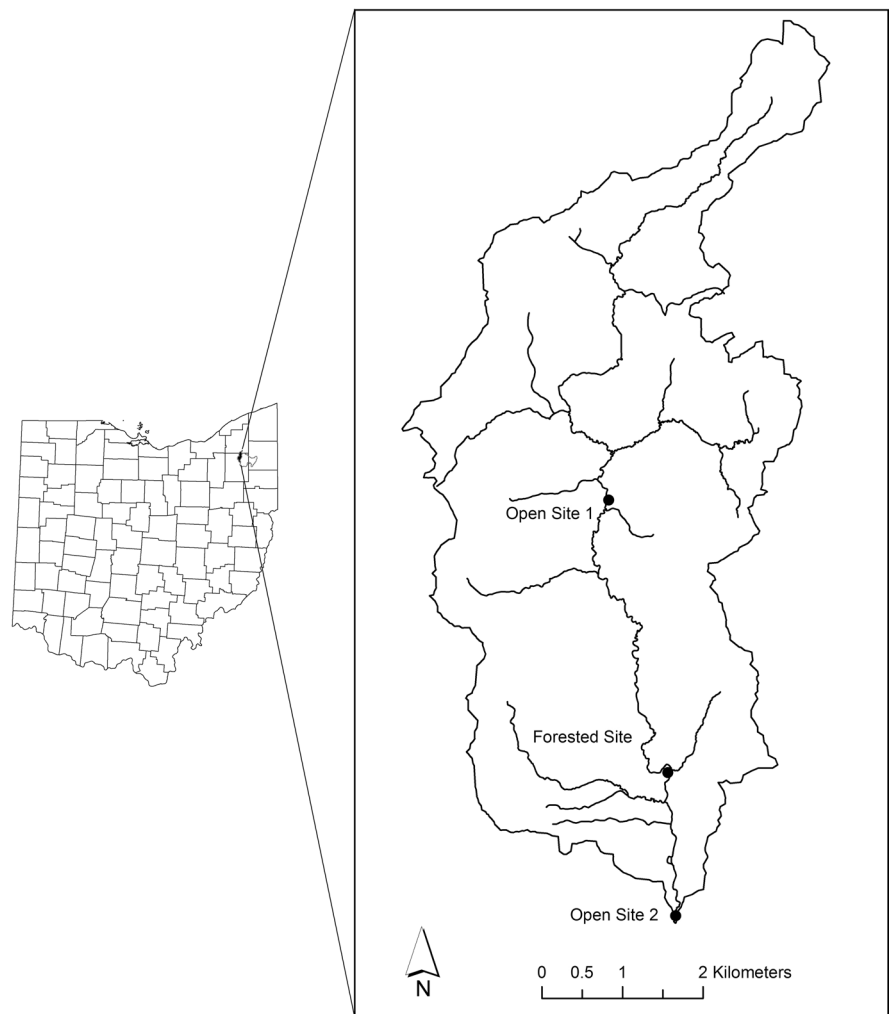
## Artificial substrates and sample processing

An artificial substrate set consisted of 20, 5.1 × 5.1 cm unglazed ceramic tiles mounted on plastic racks and secured to the stream bottom with metal stakes. Substrate sets were randomly placed in shallow riffles at each study site on 8 June 2009 and left in place for 60 days. From initial placement, tiles were collected on day (d) 2, d4, d8, d16, d32, d48, and d60. On each collection day, one tile from each set was collected for macroinvertebrates by placing a 250 μm mesh net behind the tile to capture macroinvertebrates that might be dislodged during removal. Another tile was collected for analysis of epilithic material. All tiles were secured in dark containers, placed on ice, and transported to the laboratory for analysis.

Epilithic material from one tile of each set was analyzed for periphyton biomass and chlorophyll *a*. For periphyton biomass, ½ the tile area was scraped and the slurry was filtered onto a preweighed glass fiber filter (0.45 μm pore size) and dried at 60°C until a constant weight was achieved. Filters were ignited at 500°C for 24 h, desiccated, and reweighed to obtain ash-free dry mass (AFDM). The remaining ½ tile area was scraped and filtered onto a 0.45 μm glass fiber filter. Chlorophyll *a* was extracted from filters with 90% acetone and analyzed with a spectrophotometer after correcting for pheophytin (Lorenzen, 1967).

The entire area of the second tile was scraped and the contents preserved in 70% ethanol for macroinvertebrate identification and enumeration. Macroinvertebrates were hand-sorted from organic matter

under a dissecting microscope, identified to the lowest practical taxonomic level, enumerated, and measured to the nearest 0.5 mm in length in order to estimate biomass from published length–weight regressions (Benke et al., 1999). All insect taxa were identified to genus, except Chironomidae, which were identified as Tanypodinae or non-Tanypodinae. Non-insect taxa were identified to phylum (Nematoda), class (Oligochaeta, Turbellaria), subclass (Acari), and family (Ancylidae). Taxa were then assigned to trophic groups according to information in Thorp & Covich (2009) and Merritt et al. (2008).

## Channel habitat and water chemistry

Channel width, water depth, and visual estimates of bed substrate composition were measured at 11 equally spaced transects within each site during summer 2009. Water temperature was continuously recorded at 15-min intervals with HOBO Pendant® temperature loggers (model UA-001-64; Onset Computer Corp., Bourne, MA, USA). Water velocity and depth were measured at artificial substrate locations on five occasions during the colonization interval. Conductivity, dissolved oxygen, and pH were determined from in situ readings when tiles were collected. Grab samples for nutrient analyses were collected on 27 and 31 July 2009 and 7 August 2009. Total phosphorus (TP) and nitrogen (TN) were determined with a Lachat Quik-Chem 8000 (Hach Co., Loveland, CO, USA) using in-line persulfate digestion and colorimetric methods recommended by Lachat (Quik-Chem Method 10-115-01-3-A for TP and Method 10-107-04-3-P for TN).

## Data analysis

Simple linear regression was used to determine if rates of algal resource accrual and macroinvertebrate densities and biomass increased linearly throughout the 60-day colonization period. Colonization rates were determined from slopes of significant regressions. Analysis of Covariance (ANCOVA) models were performed to test for significant differences in colonization rates among sites. Differences in rates of increase/decrease were considered significantly different if the interaction between the covariate (time) and main factor (site) in the ANCOVA model was

significant ($P < 0.05$). Slopes from significant regressions were compared with Tukey's multiple comparison. If the interaction from ANCOVA was not significant (site x time, $P > 0.05$), then the interaction term was removed and ANOVA was performed on the main site effects (Engqvist, 2005). We also performed simple and partial Pearson correlations with combined data from all study sites to examine the relationships between all taxa and trophic groups, and to explore the relative influence of time, temperature, and chlorophyll $a$ on taxa and functional feeding group abundance and biomass. All response variables were log $(x + 1)$ transformed to meet the assumptions of normality prior to analysis. Analyses were performed in SAS® v. 9.3 (SAS, Inc., Cary, NC, USA).

Non-metric multidimensional scaling (NMS) was used to identify potential differences and gradients in macroinvertebrate community composition on tiles within and among sites throughout the colonization period. The NMS was conducted using PC-ORD v. 6.0 software (McCune & Mefford, 2011). Taxa that occurred in less than 2% of samples were not included in the analysis. We used the Bray–Curtis similarity coefficient on the mean macroinvertebrate abundance from tiles on each day of the colonization period in the main matrix and the data were computed with 250 iterations, 50 real runs, and 50 randomized runs. To improve interpretation of the NMS, successional vectors were added to the ordination diagrams to explore differences in compositional changes over time at each site. Time (day during the colonization period), degree days, and algal resources from tiles were correlated with NMS axes to determine the relative influence of these variables on macroinvertebrate colonization patterns.

## Results

### Channel habitat and water chemistry

Relative to the Forested Site, the open sites had no or minimal canopy cover, and greater amounts of fine sediment (Table 1). Daily temperature ranges and mean maximum temperatures at the open sites were approximately 2–3X greater than those at the Forested Site, and accumulated degree days (ADD) increased according to stressor gradient (Table 1). TP concentrations were similar among sites, but the maximum

TN concentration detected at Open Site 1 and Open Site 2 was 2 and 7X greater than maximum concentrations at the Forested Site (Table 1).

Algal resource accrual

ANCOVA indicated significant differences in accrual rates of chlorophyll *a* and epilithic material on tiles among sites (Table 2). Since chlorophyll *a* and epilithic mass were highly correlated ($r = 0.93$, $P < 0.001$), only chlorophyll *a* was used in further analyses. Chlorophyll *a* increased linearly throughout the 60-day colonization period at all study sites and accrual rates at Open Site 2 were significantly more rapid than rates at the Forested Site, but rates at Open Site 1 were not significantly different from rates at the

other sites (Table 3; Fig. 2). By d60, chlorophyll *a* biomass at Open Site 2 was approximately 3X the amount at Open Site 1 and 12X times the amount at the Forested Site (Fig. 2). There was a significant linear relationship between chlorophyll *a* and mean maximum TN concentrations from the study sites (SLR, $r^2 = 0.99$, $P = 0.05$) (Fig. 3). Among other variables in Table 1, chlorophyll *a* also was significantly correlated with ADD ($r = 0.99$, $n = 3$, $P < 0.05$).

Macroinvertebrate richness, total density, and biomass

Twenty-one taxa, represented by four functional feeding groups—collector-gatherers, collector-filterers, scrapers, and predators—were collected from tiles during the colonization period. Nine taxa (non-Tanypodinae Chironomidae, *Simulium*, *Baetis*, *Hydroptila*, *Cheumatopsyche*, *Antocha*, Hydracarina, Tanypodinae, and *Hemerodromia*) comprised more than 90% of the total macroinvertebrate abundance at all study sites. Throughout the colonization period, Open Site 1 had the greatest taxa richness with 18 taxa, while 13 taxa were collected at both the Forested Site and Open Site 2.

ANCOVA indicated that most macroinvertebrate responses had significantly different linear rates of increase among sites (Table 2). Time to maximum richness did not show a clear increase along the resource gradient, but taxa richness increased at a faster rate at Open Site 2 (Table 3; Fig. 4a). Total macroinvertebrate abundance had a weak linear increase during the 60-day colonization period at Open Site 2 and ANCOVA indicated no difference in rates among sites (Table 3; Fig. 4b). After the site × time interaction term was removed, mean total macroinvertebrate abundance at the Forested Site was significantly less than total abundance at open sites (Table 2, ANOVA: $F_{2,60} = 27.12$, $P < 0.001$). By d60, total macroinvertebrate abundance at Open Site 2 was 4 and 8X the densities at Open Site 1 and the Forested Site (Fig. 4b). Total macroinvertebrate biomass increased linearly over time at the open sites and the rate of increase was significantly faster at Open Site 2 (Table 3; Fig. 4c). Time to maximum biomass increased along the resource gradient, and by d60, total macroinvertebrate biomass at Open Site 2 was 26X the amount at the Forested Site and 5X the amount at Open Site 1 (Table 3; Fig. 4c).

**Table 1** Habitat, physical–chemical, and nutrient variables from each study site during the 60-day colonization period

|  | Forested Site | Open Site 1 | Open Site 2 |
|---|---|---|---|
| Water velocity (cm/s) | 0.3 ± 0.0 | 0.5 ± 0.1 | 0.5 ± 0.1 |
| Tile depth (cm) | 9.4 ± 0.9 | 6.4 ± 0.8 | 7.5 ± 0.9 |
| Channel Habitat |  |  |  |
| Width (m) | 6.8 ± 1.5 | 3.7 ± 0.9 | 5.9 ± 1.7 |
| Depth (m) | 0.4 ± 0.3 | 0.2 ± 0.1 | 0.2 ± 0.2 |
| % Fine sediment | 13 ± 13 | 61 ± 29 | 44 ± 37 |
| % Canopy cover | 84 ± 14 | 1 ± 2 | 26 ± 38 |
| Physical–chemical |  |  |  |
| Conductivity (μS/cm) | 229–466 | 322–480 | 271–480 |
| DO (mg/L) | 7.7–8.6 | 7.1–10.1 | 7.7–11.3 |
| pH | 7.75–8.09 | 7.72–8.06 | 7.74–8.47 |
| Temperature (°C) |  |  |  |
| Daily mean | 18.4 ± 1.4 | 18.6 ± 2.2 | 18.7 ± 2.3 |
| Daily max | 19.4 ± 1.3 | 22.0 ± 2.0 | 22.0 ± 1.7 |
| Daily range | 2.0 ± 0.7 | 5.6 ± 1.9 | 5.3 ± 1.6 |
| ADD | 1,083 | 1,088 | 1,097 |
| Nutrients (mg/L) |  |  |  |
| TP | 0.04–0.04 | 0.03–0.05 | 0.02–0.05 |
| TN | 0.15–0.27 | 0.23–0.47 | 0.37–1.89 |

Values are means (±1SD) for habitat measures. Minimum and maximum values are reported for physical–chemical and nutrient parameters. *DO* Dissolved oxygen; *ADD* Accumulated degree days; *TP* Total phosphorous; *TN* Total nitrogen

**Table 2** Variables measured from tiles during the 60-day colonization period at each study site

| Variable | Forested Site | Open Site 1 | Open Site 2 | P value |
|---|---|---|---|---|
| Chlorophyll $a$ (mg/m$^2$) | 1.9 ± 0.5 | 5.0 ± 1.6 | 13.7 ± 3.9 | <0.0001 |
| Epilithic mass (mg AFDM/cm$^2$) | 35.0 ± 8.1 | 251.2 ± 104.8 | 233.4 ± 75.9 | <0.0001 |
| Taxa richness (taxa/cm$^2$) | 3.1 ± 0.3 | 4.9 ± 0.4 | 5.2 ± 0.5 | <0.0001 |
| Macroinvertebrate abundance (ind/cm$^2$) | | | | |
|   Total abundance | 0.52 ± 0.06 | 2.26 ± 0.46 | 3.10 ± 0.37 | 0.0924 |
|   Collector-gatherers | 0.28 ± 0.05 | 1.61 ± 0.49 | 1.18 ± 0.19 | 0.0003 |
|   Collector-filterers | 0.21 ± 0.04 | 0.51 ± 0.17 | 1.51 ± 0.31 | 0.0330 |
|     *Simulium* | 0.13 ± 0.04 | 0.43 ± 0.18 | 1.04 ± 0.33 | <0.0001 |
|     Hydropsychidae | 0.03 ± 0.01 | 0.07 ± 0.03 | 0.32 ± 0.11 | <0.0001 |
|   Scrapers | 0.00 ± 0.00 | 0.06 ± 0.03 | 0.36 ± 0.16 | <0.0001 |
|   Predators | 0.03 ± 0.01 | 0.08 ± 0.02 | 0.05 ± 0.02 | <0.0001 |
| Macroinvertebrate biomass (mg ADFM/cm$^2$) | | | | |
|   Total biomass | 0.034 ± 0.009 | 0.096 ± 0.021 | 0.363 ± 0.105 | <0.0001 |
|   Collector-gatherers | 0.001 ± 0.000 | 0.012 ± 0.004 | 0.036 ± 0.017 | 0.0010 |
|   Collector-filterers | 0.025 ± 0.009 | 0.029 ± 0.009 | 0.292 ± 0.080 | <0.0001 |
|     *Simulium* | 0.001 ± 0.001 | 0.012 ± 0.005 | 0.031 ± 0.013 | 0.0047 |
|     Hydropsychidae | 0.015 ± 0.008 | 0.017 ± 0.008 | 0.230 ± 0.080 | <0.0001 |
|   Scrapers | 0.000 ± 0.000 | 0.009 ± 0.004 | 0.030 ± 0.015 | <0.0001 |
|   Predators | 0.008 ± 0.005 | 0.047 ± 0.018 | 0.004 ± 0.003 | <0.0001 |

Values are means (±1SE) ($n = 21$). P values are for the site × interaction from ANCOVA. $P < 0.05$ indicates response variable had significantly different linear rates of increase among sites over the colonization period

## Macroinvertebrate functional feeding groups

Collector-gatherers colonized tiles by d2 and were abundant throughout the colonization period at all sites (Fig. 5a). Collector-gatherer densities increased linearly with time at the Forested Site and Open Site 2, but their rate of increase was more rapid at Open Site 2 (Table 4). During the early colonization period (d2–8), chironomid midges were the only collector-gatherers collected from tiles. By d16, the collector-gatherer *Antocha* occurred at all sites but was most abundant on tiles at open sites. As a result of *Antocha* abundance, collector-gatherer biomass increased linearly with time and at similar rates at open sites (Table 4; Fig. 5 b). Between d16 and 60, collector-gatherer biomass at the Forested Site was dominated by midges (85%) and *Antocha* (60–75%) at the open sites (Fig. 6a–f).

Collector-filterers reached maximum densities by d8, and then declined until the end of the colonization period at all study sites (Fig. 5c). Collector-filterer biomass increased linearly during the colonization period at Open Site 2 (Table 4; Fig. 5d). Between d2

and 8, *Simulium* (black flies) dominated total macro-invertebrate abundance (93–95%) on tiles at all study sites, and dominated total macroinvertebrate biomass during that time at the open sites (Fig. 6a–f). Black fly abundance decreased over time at all study sites, with a faster rate of decline at Open Site 2 (Table 4). Hydropsychid abundance and biomass increased linearly over time only at Open Site 2 (Table 4).

Scraper taxa that colonized tiles between d16 and 32 included *Hydroptila* and *Baetis* at all sites and Ancylidae at Open Site 1 (Fig. 6). Scraper abundance and biomass increased linearly at open sites, and rates of increase were more rapid at Open Site 2 (Table 4; Fig. 5e, f). The scraper contribution to total macro-invertebrate abundance and time to maximum scraper density and biomass clearly increased along the resource gradient (Table 4; Fig. 6a–f).

Predators colonized tiles early (d2 or 4) at the Forested Site and Open Site 1 but were not collected at Open Site 2 until d16 (Fig. 5g, h). Early predators (d2–8) included large-bodied *Perlesta*, which contributed 26 and 64% to total macroinvertebrate biomass at Open Site 1 and the Forested Site (Fig. 6b, d).

**Table 3** Linear regression results for response variables from tiles and time (60-day colonization period) along the resource gradient ($n = 21$ for each study site)

|  | Adj $r^2$ | $P$ | Colonization rate | Days to max |
|---|---|---|---|---|
| **Chlorophyll $a$ (mg/m$^2$)** | | | | |
| Forested | 0.64 | <0.0001 | 0.0132[A] | 32 |
| Open 1 | 0.88 | <0.0001 | 0.0210[AB] | 60 |
| Open 2 | 0.60 | <0.0001 | 0.0250[B] | 60 |
| **Taxa richness (taxa/cm$^2$)** | | | | |
| Forested | 0.19 | 0.0285 | 0.0038[A] | 16 |
| Open 1 | 0.25 | 0.0124 | 0.0033[A] | 46 |
| Open 2 | 0.67 | <0.0001 | 0.0055[B] | 32 |
| **Abundance (ind/cm$^2$)** | | | | |
| Forested | NS | | | 46 |
| Open 1 | NS | | | 46 |
| Open 2 | 0.17 | 0.0367 | 0.0038 | 60 |
| **Biomass (mg AFDM/cm$^2$)** | | | | |
| Forested | NS | | | 16 |
| Open 1 | 0.44 | 0.0006 | 0.0012[A] | 46 |
| Open 2 | 0.60 | <0.0001 | 0.0050[B] | 60 |

NS indicates no significant linear relationship with time. Rates (unit day$^{-1}$) were determined from the slope of the linear regression line. Different letters indicate significant differences in rates following Tukey's post hoc tests. Days to max is the day when maximum values were detected

*Hemerodromia*, Hydracarina, and Tanypodinae occurred at all sites, *Atherix* and *Chrysops* occurred only at open sites, and *Nigronia* occurred only at the Forested Site. Predator abundance increased linearly at all sites, but the rates of increase did not correspond to the resource gradient (Table 4; Fig. 5g, h). However, time to maximum predator density decreased along the gradient (Table 4). Late-colonizing predators at Open Site 1 included large *Atherix,* which contributed to the linear increase in predator biomass at Open Site 1 (Table 4; Figs. 5h, 6c, d).

When data from all sites were combined, no negative correlations between taxa or trophic groups were detected. Most macroinvertebrate responses had similar correlations with time and ADD, since these variables were highly correlated ($r = 0.99$, $n = 21$, $P < 0.0001$). With the exception of black flies, abundance and biomass of most macroinvertebrate primary consumers had stronger relationships with
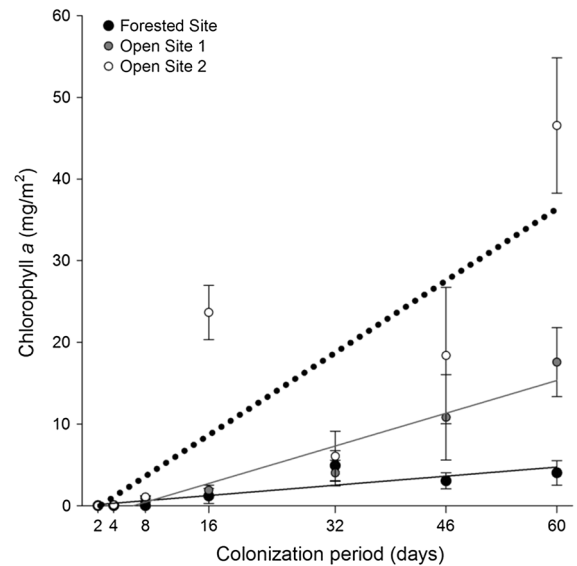


**Fig. 2** Chlorophyll $a$ on tiles over the 60-day colonization period at each study site ($n = 3$ tiles). Values are mean ± 1SE. *Lines* indicate significant linear increase over the 60 days (*black line* = Forested Site; *gray line* = Open Site 1; *dashed line* = Open Site 2)



Chlor $a$ = -0.907+(16.315 x TN)
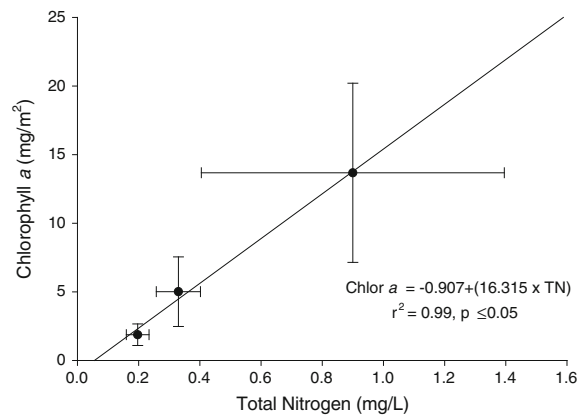$r^2$ = 0.99, p ≤0.05

**Fig. 3** Relationship between mean ± 1SE total nitrogen concentrations in stream water ($n = 3$ dates) and chlorophyll $a$ standing crop on tiles ($n = 7$ dates) during the colonization period at the study sites

chlorophyll $a$ biomass than with time and ADD, and the relationships remained significant when time and ADD were held constant (Table 5).

Macroinvertebrate community composition

NMS produced a two-dimensional solution with a final stress value of 9.25. NMS axis 1 represented 55% of the variation in the community data and NMS axis 2

**Table 4** Linear regression results for response variables from tiles and time (60-day colonization period) along the resource gradient ($n = 21$ for each study site)

| | Abundance | | | | Biomass | | | |
|---|---|---|---|---|---|---|---|---|
| | Adj $r^2$ | $P$ | Colonization rate | Days to max | Adj $r^2$ | $P$ | Colonization rate | Days to max |
| Collector-gatherers | | | | | | | | |
| Forested | 0.40 | 0.0013 | 0.0022[A] | 46 | | NS | | 46 |
| Open 1 | | NS | | 46 | 0.26 | 0.0105 | 0.0002[A] | 46 |
| Open 2 | 0.47 | 0.0004 | 0.0060[B] | 16 | 0.20 | 0.0241 | 0.0007[A] | 46 |
| Collector-filterers | | | | | | | | |
| Forested | | NS | | 46 | | NS | | 46 |
| Open 1 | | NS | | 46 | | NS | | 46 |
| Open 2 | | NS | | 60 | 0.58 | <0.0001 | 0.0034 | 60 |
| *Simulium* | | | | | | | | |
| Forested | 0.22 | 0.0184 | −0.0006[A] | 8 | | NS | | 8 |
| Open 1 | 0.29 | 0.0074 | −0.0044[A] | 8 | | NS | | 8 |
| Open 2 | 0.37 | 0.0021 | −0.0073[B] | 8 | 0.17 | 0.0373 | −0.0005 | 8 |
| Hydropsychidae | | | | | | | | |
| Forested | | NS | | 46 | | NS | | 46 |
| Open 1 | | NS | | 46 | | NS | | 46 |
| Open 2 | 0.57 | <0.0001 | 0.0050 | 60 | 0.67 | <0.0001 | 0.0043 | 60 |
| Scrapers | | | | | | | | |
| Forested | | NS | | 16 | | NS | | 32 |
| Open 1 | 0.18 | 0.0332 | 0.0010[A] | 46 | 0.16 | 0.0401 | 0.0002[A] | 46 |
| Open 2 | 0.51 | 0.0002 | 0.0059[B] | 60 | 0.42 | 0.0008 | 0.0009[B] | 60 |
| Predators | | | | | | | | |
| Forested | 0.33 | 0.0040 | 0.0006[A] | 60 | | NS | | 8 |
| Open 1 | 0.62 | <0.0001 | 0.0013[B] | 46 | 0.40 | 0.0012 | 0.0010 | 60 |
| Open 2 | 0.49 | 0.0003 | 0.0010[AB] | 32 | | NS | | 60 |

NS indicates no significant linear relationship with time. Rates (unit day$^{-1}$) were determined from the slope of the linear regression line. Different letters indicate significant differences in rates following Tukey's post hoc tests. Days to max is the day when maximum values were detected

represented an additional 30% (Fig. 7). The colonizing fauna from the Forested Site and Open Site 2 separated considerably from each other in ordination space, while Open Site 1 was more variable and intermediate to the other sites (Fig. 7a). Collector-gathering midges had the strongest positive correlation with axis 1 ($r = 0.80$). Eight other taxa also had positive axis 1 correlations ($r = 0.43–0.60$). The predator *Perlesta* had a negative correlation ($r = −0.45$) with axis 1 and *Simulium* had a strong negative correlation ($r = −0.87$) with axis 2. NMS axis 1 scores were positively correlated with chlorophyll $a$ ($r = 0.51$) while axis 2 scores were positively correlated with ADD ($r = 0.45$) and time ($r = 0.29$) (Fig. 7a). Within each site, the greatest degree of change in community composition occurred during the early colonization period (d2–16). Reversed trajectories with axis 2 on d8 at all sites resulted from maximum black fly abundance (Fig. 7b). The direction of successional vectors along each axis indicates the relative influence of chlorophyll $a$, ADD, and time on macroinvertebrate colonization at each site (Fig. 7a, b). The chlorophyll $a$ influence at Open Site 2 became especially apparent on d32 when the successional vector reversed its trajectory along axis 2 and moved forward along axis 1 (Fig. 7a, b).
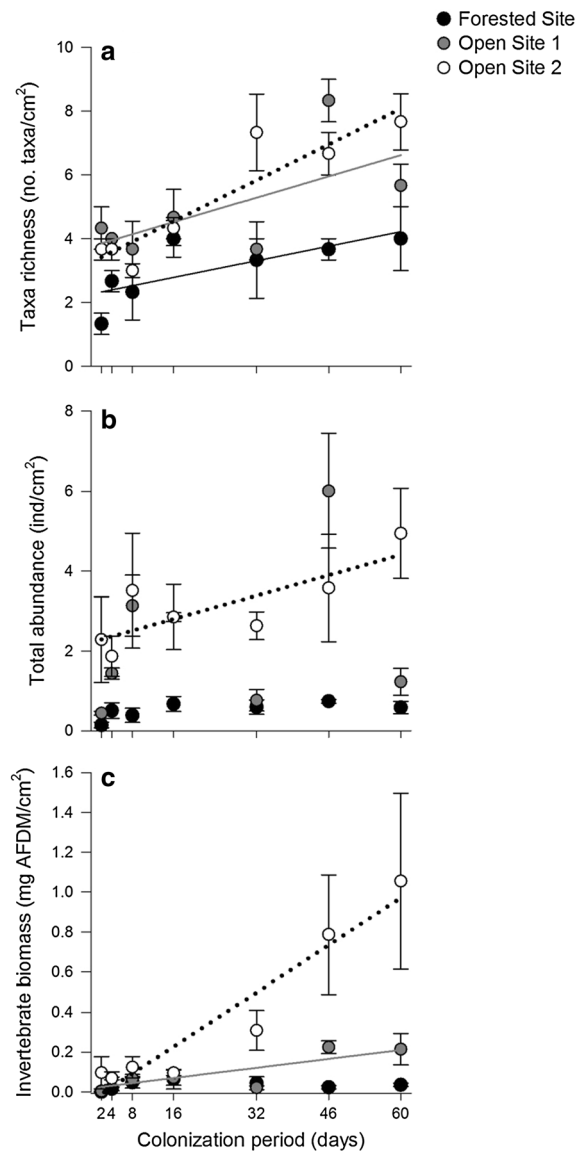
Fig. 4 Macroinvertebrate taxa richness (a), abundance (b), and biomass (c) from tiles at each study site (*n* = 3 tiles) during the 60-day colonization period. Values are means ± 1SE. *Lines* indicate significant linear increase over the 60 days (*black line* = Forested Site; *gray line* = Open Site 1; *dashed line* = Open Site 2)

## Discussion

Accumulated temperatures, TN concentrations, and standing stocks of chlorophyll *a* biomass on substrates increased along the algal resource gradient as we expected. Total macroinvertebrate biomass and the abundance and biomass of scrapers had high

correlation with algal accrual and clearly increased along the gradient. Most other macroinvertebrate metrics showed no clear increase along the gradient (e.g., total macroinvertebrate abundance, collector-gatherer abundance/biomass, predator abundance), and some metrics (e.g., predator biomass, abundance and biomass of hydropsychids) had relatively rapid rates of increase at only one site, which likely influenced the colonization rates of other taxa at those sites.

Total biomass, rather than abundance, better reflected the resource gradient since biomass was not influenced by high densities of small-bodied black flies and chironomids. Relatively high densities of black flies during early colonization and fluctuating midge densities at the open sites resulted in relatively slow or no increase in total macroinvertebrate abundance during the colonization period. Black flies are opportunistic taxa that prefer clean substrates for attachment (Chutter, 1968; Hemphill & Cooper, 1983). Early colonization by black flies—followed by their quick declines—has been attributed to the development of unfavorable conditions as potential competitors (e.g., hydropsychids) and epilithic layers increase (Hemphill & Cooper, 1983; Ciborowski & Clifford, 1984; Downes & Lake, 1991). In our study, pupal cases were absent and we found no correlations between black flies and both chlorophyll *a* and other taxa. These findings suggest that black fly declines between d8 and 16 probably resulted from the development of unfavorable substrate conditions, rather than emergence or negative interactions with other taxa.

Lack of continuous increases in macroinvertebrate biomass over the colonization period at the Forested Site resulted from low densities of primary consumers. Food webs in temperate forested stream reaches are detrital based and supported by inputs of forest litter from the riparian zone (Fisher & Likens, 1973; Minshall et al., 1983b; Wallace et al., 1999). Many taxa in forested stream reaches are adapted for feeding on leaf litter and detritus that accumulates in the interstitial spaces of stream beds and debris dams (Wallace & Webster, 1996). Tiles at the Forested Site probably lacked preferred food for taxa that are adapted for feeding on terrestrial litter inputs rather than periphyton. Furthermore, macroinvertebrate colonization rates are influenced by the densities, mobility, and composition of the pool of available

**Fig. 5** Macroinvertebrate functional feeding group abundance (**a**, **c**, **e**, **g**) and biomass (**b**, **d**, **f**, **g**) from tiles at each study (*n* = 3 tiles) during the 60-day colonization interval. Values are means ± 1SE. *Lines* indicate significant linear increase over 60 days (*black line* = Forested Site; *gray line* = Open Site 1; *dashed line* = Open Site 2)
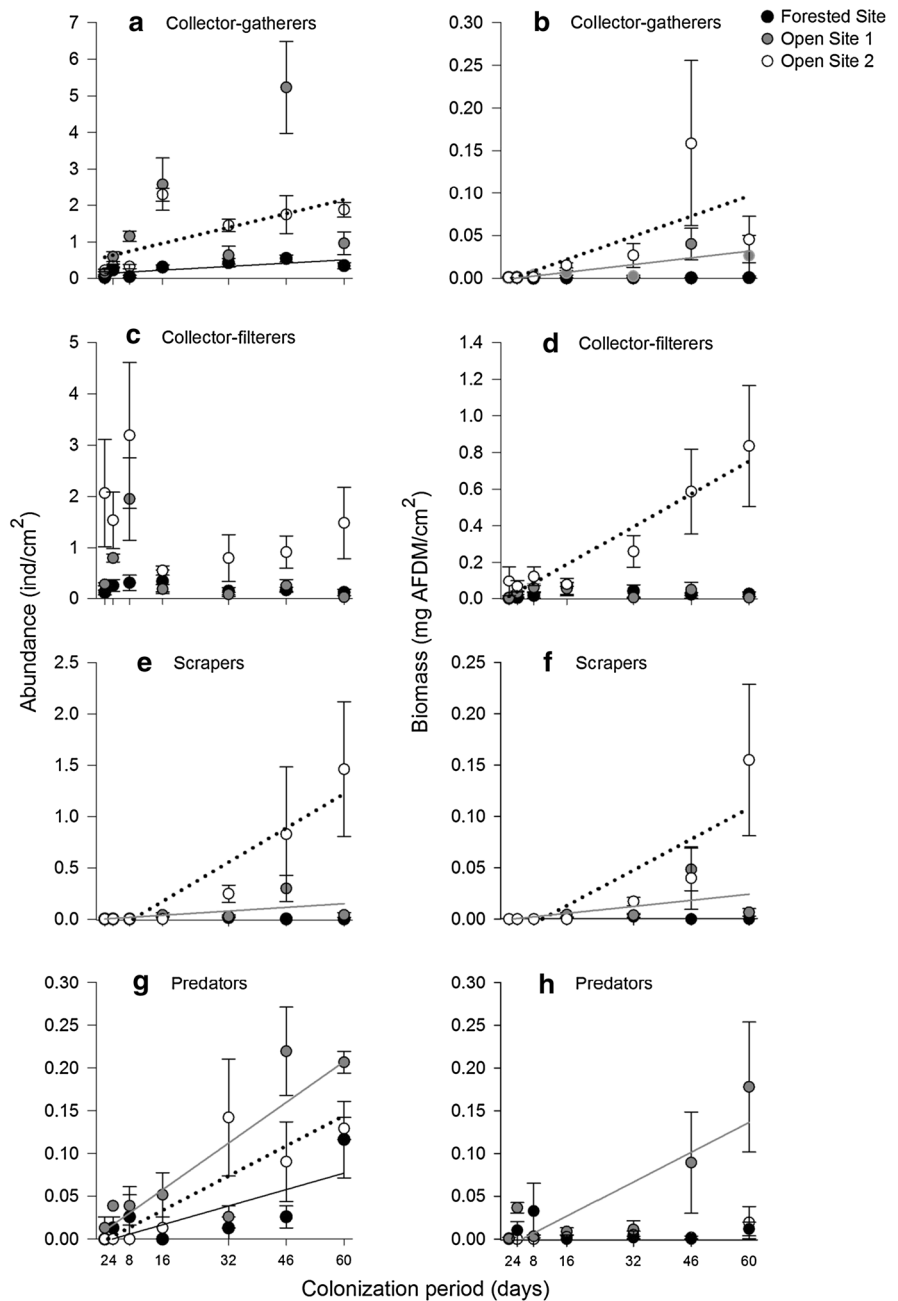


colonizers (Shaw & Minshall, 1980; Benson & Pearson, 1987; Robinson et al., 1993). Several studies have shown that macroinvertebrate densities and biomass (or both) can be greater in open canopy stream sections presumably as a result of altered food resources from increased primary production (Hawkins et al., 1982; Behmer & Hawkins, 1986; Dudgeon & Chan, 1992; Quinn et al., 1997). Decreased

densities in riffles, as a result of decreased primary production in the reach, might also explain the relatively slower colonization by macroinvertebrates at the Forested Site.

The biomass response to the gradient became apparent on d32 when total macroinvertebrate biomass at Open Site 2 differed from the other sites due to increases in hydropsychid densities since d16.

**Table 5** Results from simple and partial Pearson correlations between mean macroinvertebrate abundance (Abd) and biomass (Bio), time (day), degree days, and mean chlorophyll $a$ biomass (mg/m$^2$) from each sampling date for all sites combined ($n = 21$)

| | Simple correlations | | | | | | Partial correlations | |
| | Time | | Degree days | | Chlorophyll $a$ | | Chlorophyll $a$ | |
| | $r$ | $P$ | $r$ | $P$ | $r$ | $P$ | $r$ | $P$ |
|---|---|---|---|---|---|---|---|---|
| Abundance | 0.32 | NS | 0.34 | NS | 0.51 | 0.0179 | 0.55 | 0.0152 |
| Biomass | 0.53 | 0.0141 | 0.53 | 0.0127 | 0.70 | 0.0004 | 0.59 | 0.0075 |
| Collector-gatherers | | | | | | | | |
| Abd | 0.63 | 0.0023 | 0.64 | 0.0018 | 0.73 | 0.0002 | 0.55 | 0.0151 |
| Bio | 0.57 | 0.0076 | 0.56 | 0.0081 | 0.77 | <0.0001 | 0.66 | 0.0021 |
| Collector-filterers | | | | | | | | |
| Abd | −0.34 | NS | −0.33 | NS | −0.14 | NS | 0.36 | NS |
| Bio | 0.33 | NS | 0.34 | NS | 0.51 | 0.0187 | 0.49 | 0.0329 |
| *Simulium* | | | | | | | | |
| Abd | −0.70 | 0.0004 | −0.68 | 0.0006 | −0.58 | 0.0061 | 0.11 | NS |
| Bio | −0.53 | 0.0134 | −0.52 | 0.0162 | −0.46 | 0.0345 | 0.00 | NS |
| Hydropsychidae | | | | | | | | |
| Abd | 0.48 | 0.0276 | 0.49 | 0.0254 | 0.66 | 0.0012 | 0.56 | 0.0119 |
| Bio | 0.53 | 0.0129 | 0.54 | 0.0119 | 0.68 | 0.0007 | 0.53 | 0.0200 |
| Scrapers | | | | | | | | |
| Abd | 0.62 | 0.0028 | 0.61 | 0.0031 | 0.73 | 0.0002 | 0.49 | 0.0329 |
| Bio | 0.56 | 0.0087 | 0.55 | 0.0100 | 0.71 | 0.0003 | 0.54 | 0.0171 |
| Predators | | | | | | | | |
| Abd | 0.66 | 0.0010 | 0.65 | 0.0013 | 0.57 | 0.0071 | −0.01 | NS |
| Bio | 0.31 | NS | 0.30 | NS | 0.28 | NS | 0.04 | NS |

Values are correlation coefficients ($r$) followed by $P$ values. Partial correlations were determined by holding time and degree days constant

Collector-filtering hydropsychids usually increase on substrates after the development of a periphyton layer because they prefer irregular surfaces for attachment of their retreats (Hynes, 1975; Hemphill & Cooper, 1983; Mackay, 1992). Greater chlorophyll $a$ standing crops on d16 at Open Site 2 suggests that favorable habitat for hydropsychids developed earlier than at other sites. Hydropsychids can facilitate colonization of other taxa because their retreats enhance habitat, substrate complexity, and food resources (Diamond, 1986; Englund, 1993; O'Connor, 1993; Nakano et al., 2005). Cardinale et al. (2001) showed that early colonization of substrates by *Ceratopsyche bronta* resulted in greater abundance and biomass of all macroinvertebrates after a 30-day colonization period. These attributes of hydropsychids—coupled with their high colonization rates—may account for the more rapid increase in taxa richness noted at Open Site 2.

Rapid hydropsychid colonization rates at Open Site 2 could have also resulted from greater densities and production in riffle habitats. Elevated temperatures and improved food quality, such as algal-derived seston, may increase the abundance and production of collector-filterers (Wallace & Merritt, 1980). The discrepancy between hydropsychid abundance and biomass between d32 and 46, and the strong relationship between hydropsychid biomass and time (rather than abundance and time), indicates that an increase in their biomass was possibly due to growth or selective replacement of small individuals by larger individuals. Though hydropsychids can facilitate colonization of certain taxa, they can also be defensive and territorial, thus preventing the establishment of other taxa (Englund & Olsson, 1990; Hemphill, 1991; Englund, 1993). Relatively large hydropsychids may have excluded other large taxa, which might explain why

**Fig. 6** Macroinvertebrate relative abundance (a, **c**, **e**) and biomass (**b**, **d**, **f**) on tiles from study sites throughout the 60-day colonization period
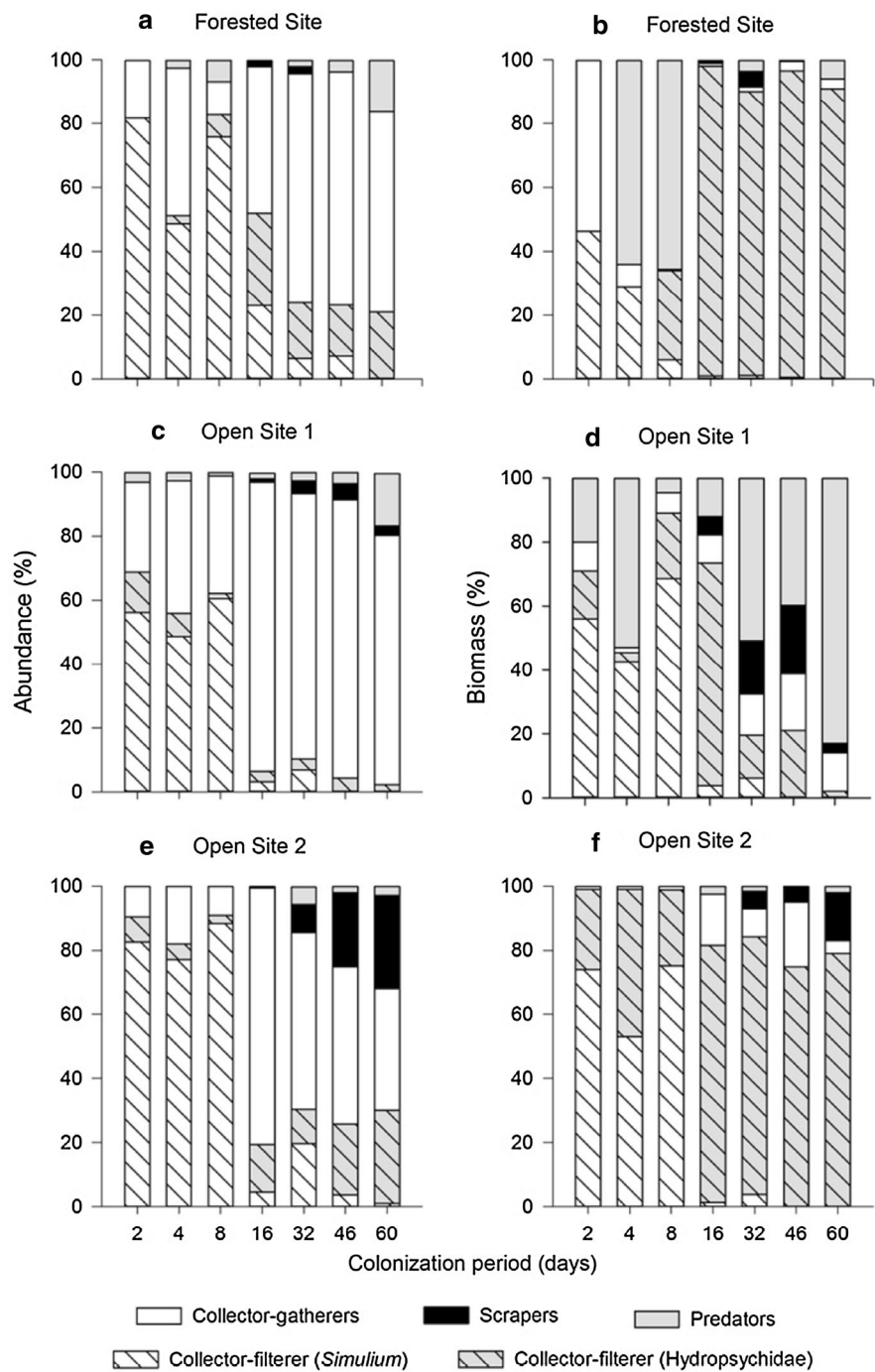


most predators from tiles at Open Site 2 were relatively small (e.g., mites) compared to large predators at other sites (e.g., *Atherix* and *Nigronia*).

Scrapers also contributed to biomass increases on tiles between d32 and 60 at the open sites. The high correlation between scraper abundance and biomass suggests continuous colonization by individuals. The scraper response to algal accrual in this study is not surprising since results from field studies have shown direct relationships between scrapers and algal

**Fig. 7** Non-metric
multidimensional scaling
results. *Circles* represent
mean macroinvertebrate
densities ($n = 3$ tiles) on
each day of the colonization
period. **a** Biplot overlay
shows the correlation of
time, degree days, and
chlorophyll *a* with
ordination axes 1 and 2—
length of vectors reflects the
magnitude of the correlation
with each axis. **b** Time
trajectories show how
macroinvertebrate
community composition
shifted along axes over the
60 day colonization
period—*numbers* next to
*circles* indicate day during
the colonization period
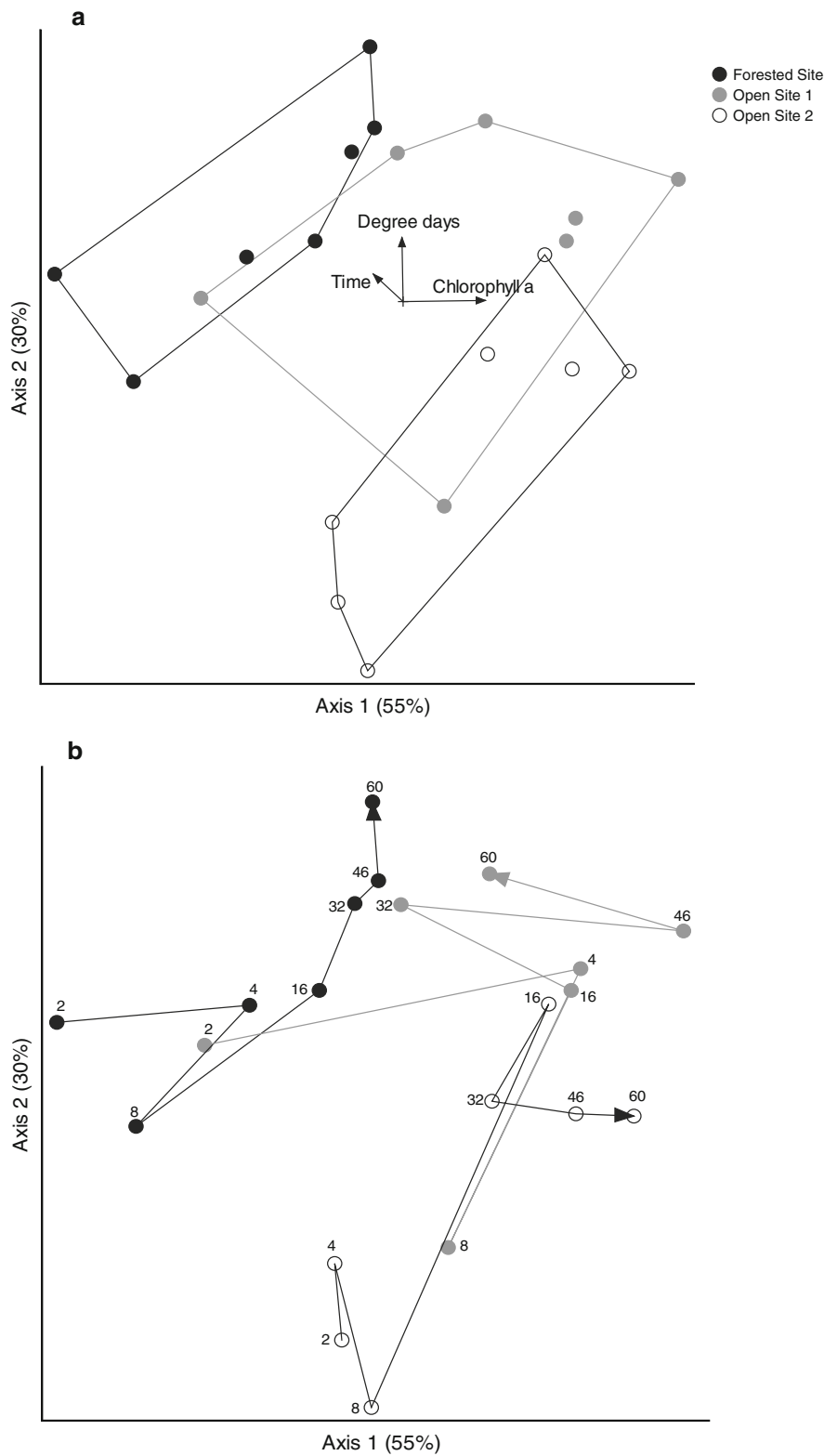
densities (Wallace & Gurtz, 1986; Richards & Minshall, 1988; Dudgeon & Chan, 1992). Further, in small-scale colonization studies, scraper densities on substrates can be tightly coupled with their algal food resources, and scraper declines have been attributed to food depletion by their grazing activity (Lamberti & Resh, 1983). Food depletion could explain the early decline in scraper densities at the Forested Site where scraper abundance declined following decreases in chlorophyll *a*. However, food depletion is an unlikely explanation for scraper declines on d46 at Open Site 1 since algal resources were still accruing through d60. The increase in macroinvertebrate biomass during the mid- to late-colonization period at Open Site 1 also resulted from increased predator densities and then replacement of smaller predators by the large predator *Atherix*. On d60, several large *Atherix* and smaller predators were collected from every tile at this site. Though we did not detect significant negative correlations between taxa, abundance of large predators on d60 corresponding with declines in densities of all primary consumers may simply be due to predation at Open Site 1. Predators have been shown to influence prey densities on substrate patches in streams (Lancaster et al., 1991). At Open Site 2, continuous increases in algal resources and scraper colonization throughout the mid- to late-colonization period suggests that food resources were not limiting.

With the exception of predators, the timing and sequence of colonization was similar among sites and did not appear to be directly influenced by resource accrual. The apparent absence of predators, especially *Perlesta*, during the early colonization period at Open Site 2 is puzzling since data from previous benthic collections indicated its presence in riffles following canopy removal (Braccia, unpublished data). Given our small sample size, we are uncertain if *Perlesta* absence resulted from a sampling artifact or factors associated with more rapid resource accrual. Although we did not detect significant negative correlations between taxa in this study, the presence of *Perlesta* at the Forested Site and Open Site 1 could have altered colonization rates of other taxa during the early colonization period because predaceous stonefly larvae can reduce immigration rates of prey taxa on substrate patches (Peckarsky & Dodson, 1980; Peckarsky, 1985).

Total macroinvertebrate densities and biomass did not appear to stabilize on tiles at Open Site 2, as indicated by maximum values on the last day of the colonization period. Maximum densities and biomass on d60 resulted from continuous increases in the abundance and biomass of scrapers and hydropsychids through the last day of the colonization period at Open Site 2. Over a 65-day colonization interval in a forested stream, Baer et al. (2001) also found lack of stabilization in macroinvertebrate densities on substrates, which they attributed to continuous increases in resource accumulation on artificial substrates. Given that scraper densities can increase with algal resources on substrates (Feminella & Hawkins, 1995), the clear increase in day to maximum scraper abundance and biomass along the stressor gradient provides some evidence that stabilization times might have been delayed as a result of differences in algal accrual rates among sites. The negative trend between day to maximum predator abundance and the resource gradient suggests that predators may have also been altered by algal accrual rates. Shorter stabilization times for predator abundance at the open sites could have resulted from interactions with other taxa (such as hydropsychids), more rapid rates of prey accumulation, or reduced predator drift rates. Results from experimental studies have shown that macroinvertebrate emigration rates (via drift) may be low in stream areas where food resources are abundant (Richardson, 1991; Hinterleitner-Anderson et al., 1992; Siler et al., 2001). If predators drift less where algal resources and prey are abundant, then predators should have encountered tiles less frequently, which might explain their delayed arrival on tiles at Open Site 2.

Results from correlation and ordination analyses suggest that the abundance and biomass of macroinvertebrate primary consumers on substrates mainly increased with chlorophyll *a* biomass, though time and temperature were also important. The total macroinvertebrate biomass response to the gradient was partly driven by colonization of primary consumers that are favorably influenced by algal resources as food or habitat (e.g., scrapers and hydropsychids), which further suggests that algal accumulation was relatively more important than time and temperature. The factors that influence benthic algal biomass in wadeable streams are complicated, and include light, temperature, nutrients, discharge, and macroinvertebrate grazing (Dodds & Welch, 2000). Our study was not designed to determine factors that limit benthic algae in Silver Creek, so we are unable to clearly identify

whether greater chlorophyll *a* biomass and accrual rates resulted from elevated light, nutrients, temperature, or a combination of these factors. However, cattle access and nearby row crop agriculture corresponded with elevated TN concentrations, greater standing stocks of algal biomass, and more rapid colonization of substrates by certain taxa (e.g., hydropsychids) and trophic groups (e.g., scrapers) at Open Site 2. These results might suggest that TN contributed to increased primary productivity, which in turn resulted in increased rates of macroinvertebrate colonization. Recent experimental evidence also suggests that addition of nutrients can alter macroinvertebrate community responses to small-scale disturbance by changing the structure of primary consumer assemblages (Gafner & Robinson, 2007).

Land use within watersheds can introduce multiple stressors to stream ecosystems (Ormerod et al., 2010). Although findings from artificial substrate studies have revealed much about the colonization and establishment of macroinvertebrate communities following small-scale disturbance in streams, the influence of stressors—such as elevated temperature and nutrients—on macroinvertebrate colonization dynamics have not been widely studied. Understanding how stressors alter the colonization and establishment of macroinvertebrate communities on benthic habitats could improve our understanding of the macroinvertebrate community structure in impaired streams and increase our chances for successful stream restoration. This study provides a description of macroinvertebrate community colonization in a perennial stream segment with patches of open canopy and agricultural land use along its riparian corridor. Our results show that continuous increases in algal resources on substrates and elevated temperatures in surrounding stream reaches can result in more rapid colonization of substrates by certain taxa and trophic groups and increase the stabilization times for total macroinvertebrate densities and biomass. These results lend support to Robinson et al.'s (1990) suggestion that periphyton might account for highly variable stabilization times in colonization studies and provides evidence that algal accumulation and macroinvertebrate colonization of substrates can vary according to canopy cover and adjacent land use within a stream segment.

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