Impact of Light Intensity on Habitat Preference of Macroinvertebrates in Carp Creek

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General Ecology

INTRODUCTION

Among nature lovers and scientists alike, biologically diverse ecosystems are consistently more desirable than areas with few species. When planning a vacation, the avid hiker or camper will choose a location with the most opportunities to experience flora and fauna in their natural habitats. Biologically diverse, healthy ecosystems have greater habitat stability and provide valuable services every day. The fibers for our textiles, the basis for 90% of modern pharmaceuticals – even fresh water for crops, bathing, and drinking; these are just the beginning of a long list of services provided by ecosystems (Turner 2007; ESA 2000).

Conserving biodiversity has become a global priority in the face of climate change, both to preserve ecosystem services and to protect the world's organisms (Geist 2011). Biodiversity is positively correlated with the stability of communities (Arthington 2010). The greater the variety of species in a given ecosystem, the greater the likelihood that at least one of them will be able to adapt to changes in that system; the survival of one species may be dependent on the variety of its neighbor species (Kormondy 1996). In the simplest sense, biodiversity is a measure of two variables: the variety of species inhabiting a particular area (species richness) and their distribution within the ecosystem (evenness) (Odum 1971). On a local scale, biodiversity is strongly influenced by variation in abiotic factors, since co-occurring species often prefer different combinations of light, moisture, temperature, and soil composition (Cushing & Allan 2001). With vast alterations to our global climate predicted for the future, it is critical to maintain high local biodiversity, as it may be a community's main defense against species loss.

Freshwater ecosystems provide particularly important services. Not only are they the source of much drinking water, but they also provide the foundation of global food production, from fisheries to agriculture (Arthington 2010). The total surface area of freshwater in the world is 5-10 million square kilometers - much smaller than both the marine (361 million square kilometers) and terrestrial environments (138 million square kilometers) (Strayer 2006). Despite this disparity in surface area, inland waters contain higher species diversity than their marine counterparts (Angelier 2003): up to 10% of all animal species are thought to live in freshwater (Geist 2011) and many others depend on freshwater organisms as their food source. Aquatic microorganisms form the basis of many food chains, and many photosynthetic freshwater algae are vital primary producers in these systems. Clearly, freshwater ecosystems are an indispensable part of the biosphere. Nevertheless, aquatic species that are responsible for providing freshwater quality, especially invertebrates, are often overlooked and underappreciated (Stayer 2006). Despite laudable efforts at creating terrestrial conservation plans, little effort has been placed on creating such schemes for marine and freshwater ecosystems (Brooks *et al.* 2006).

Invertebrates play a vital role in the proper functioning of freshwater ecosystems. By regulating rates of primary production and decomposition, they affect nutrient cycling, water clarity, and water quality (Stayer 2006). Furthermore, macroinvertebrates play a critical role in the aquatic food chain (Strayer 2006). Thirteen orders of insects spend a portion of their life cycle in freshwater ecosystems, and comprise at least half of the aquatic invertebrate community (Cushing & Allan, 2001). Most of these are endemic to their specific freshwater habitat and are not found in marine ecosystems (Angelier 2003). Since more than half of the known species on Earth are insects, the higher biodiversity of freshwater than marine ecosystems can be attributed to their insect inhabitants (Kormondy 1996). Despite the importance of freshwater invertebrates, little is known about the diversity and distribution of even the best-studied groups (Stayer 2006). By better understanding the factors contributing to high invertebrate biodiversity, we will be able to implement more effective conservation strategies to protect freshwater ecosystems and their services.

Although rivers and streams may appear to be homogenous ecosystems, they are actually composed of a patchwork of habitats. This heterogeneity is determined by the variation of many abiotic factors; water velocity, temperature, dissolved oxygen, pH, and substrate all vary from the source of the river to its mouth. Furthermore, factors like temperature and dissolved oxygen both influence species range as well as trends in life cycle (i.e. growth and energy use) (Townsend 1980). Generally, water velocity decreases with distance from the headwaters; rocks and logs increase friction, thus slowing overall stream speed (Kormondy 1996). Velocity in turn influences various other elements of the riverine system. For example, water velocity determines which substrates will be deposited and which will flow farther downstream. This riverbed architecture is correlated with aquatic plant species composition, potentially supporting a specific array of macroinvertebrates (Townsend 1980). Furthermore, variation in these abiotic factors has the potential to create patchy regions within streams and rivers, thus forming distinct niches and increasing overall species diversity.

Of these abiotic factors, little is known about the potential impacts of variable light intensity on stream biodiversity. Since sunlight directly impacts primary productivity and thereby, food and nutrient availability, the amount of light hitting the water may affect the biotic composition of a stream (Cushing & Allan 2001). Therefore, it is possible that sunny and shady parts of the same stream may provide suitable habitat for different species, including macroinvertebrates. As such, a range of light intensities would increase overall stream biodiversity.

In this study we explore whether variation in light intensity creates environmental heterogeneity and thereby results in enhanced macroinvertebrate biodiversity within a local stream, Carp Creek. Specifically, we examine the effect of light intensity on:

1. The number of individuals within different of macroinvertebrate taxa
2. The total number of macroinvertebrates,
3. The total number of macroinvertebrate taxa, and
4. Overall macroinvertebrate biodiversity.

MATERIALS AND METHODS

Site Selection

Our study was conducted in Carp Creek near Pellston, Michigan. We chose this creek because it contains a large number of both sunny and shaded areas in close proximity to each other, and because it contains many fallen logs likely to provide suitable habitat for invertebrates (Cushing 2001).

To determine whether light intensity affects macroinvertebrates in streams we chose 12 sites to sample along Carp Creek. Six of the sites were classified as “sunny sites” and six were classified as “shaded sites.” Sunny sites had no obstruction from overhanging foliage and shaded sites had shade from overhanging or fallen trees. Sites classification was based on the presence of sun/shade between 11:30 and 15:30, peak hours of sunlight in this region in late May and early June. We assumed conditions during these hours would apply for the majority of the day.

We quantified the amount of sunlight at each site using a lux meter; all sunny sites had a lux of 1 and all shaded sites fell within the range of 102 to 981 lux. Also, since Carp Creek flows north and south, we selected the shaded sites closer to the west bank of the creek to increase the probability that they remained shaded after 15:30.

Uneven river substrate creates a more favorable environment for macroinvertebrates in higher velocity portions of the stream (i.e. upstream) than do sand and soil substrates (Kormondy 1996). This is especially true of grooved, secure substrates that provide stability and lower water velocity due to friction (Way 1995). On average, jagged, uneven surfaces (such as logs) support twice the density of macroinvertebrates compared to a smooth substrate (Way 1995). Therefore, we decided to sample on submerged, suspended logs in the creek.

Six pairs of sites were identified, each consisting of one shaded and one sunny submerged log. To eliminate some potentially confounding variables, pairs were chosen to be similar in average current velocity (+/- .25 m/s) and depth from the water surface to the top of the log (+/- 4 cm). Water velocity was determined using the average of three measures using a velocity meter, and a meter stick was used to measure depth from the surface. Other variables controlled during site selection were dissolved oxygen content (81.5%-86.1%), temperature (13.5-15.0°C), and pH (8.21-8.80). These variables were not used for in pairing, since their small variation within our sampling area was judged unlikely to affect macroinvertabrates (K. Slavik, personal communication). To reduce potential impacts from the shoreline soil and vegetation, we consistently chose logs suspended over sandy soil. We also chose logs that were perpendicular to current flow in order to keep the impact of current on these substrates the same.

Sampling Technique

Once logs were paired, we took their DBH to determine a fixed sampling area consistent with the smallest log in our set. Our sampling area was 96 cm^2; on wider logs we used an 8 cm x 12 cm stencil and on narrower logs we used one that was 6 cm x 16 cm. A transparent stencil was attached using pushpins or held in place by the scraper. Two of us were positioned downstream of the log to avoid contaminating the sample by disturbing the riverbed. Sampling began with the log furthest downstream and continued upstream, also to minimize contamination of samples. One person began by positioning a Surber Sampler against the downstream face of the log, making sure the top remained above the surface and the bottom was suspended below the bottom of the log. Viewing the log through a glass bottom bucket, the other person used a putty knife to scrape the fixed area on the upstream side of the log down to the bark. Then, a squirt bottle was filled with water inside the Surber Sample to keep the sample pure. The sampler was emptied, scraped, and rinsed into a tray. The substrate was then poured through a funnel into individual bottles. Each pair of sites was sampled twice over a total of four days and, within each sample period, logs in the same pair were sampled within two hours of each other. The first round of samples was taken the week of May 27; on May 30 we sampled the first three pairs and on June 3 we sampled the remaining three. The second round of samples was taken the following week; two pairs were sampled on June 5 and four pairs on June 6.

Sample Analysis

Taxonomic and organismal abundance of sunny and shaded sites was done immediately after collection to reduce error from specimen mortality. Each sample was emptied into a tray and thoroughly sorted to collect all macroinvertebrates. Organisms were removed into petri dishes using eyedroppers and forceps and then examined under a dissecting microscope. Where possible, the organisms were identified by to order; some, such as blackfly and midge, were identified to genus.

Statistical Analysis

To determine whether samples from our first and second sampling periods could be combined for analysis, we ran paired t-tests to see if there was significant difference in sun versus shade within only our first sample and within only our second sample. Since there was only one significant difference (mayflies), we combined our data from our first and second sampling to increase sample size and have a more representative sample for the remainder of our statistical analyses.

Effect of light intensity on the number of individuals within different macroinvertebrate taxa

To determine whether the number of individuals differed between sunny and shaded areas, we ran paired t-tests comparing each taxon in sun vs. shade samples.

Effect of light intensity on the total number of macroinvertebrates

To determine whether the total number of macroinvertebrates varied between the sunny and shaded samples, we ran paired t-tests comparing the total number of individuals in sun vs. shade samples.

Effect of light intensity on the total number of macroinvertebrate taxa

To determine whether the total number of macroinvertebrate taxa differed between sunny and shaded sites, we ran paired t-tests comparing the total number of taxa in sun vs. shade samples.

Effect of light intensity on overall macroinvertebrate diversity

To determine if biodiversity was enhanced by patchiness of sunny and shaded areas along Carp Creek, we calculated the Shannon-Weiner Index for sun samples and for shade samples. We then combined the sun/shade samples and calculated the Shannon-Weiner index to reflect the biodiversity of a "patchy" stream. We compared these H' values to infer whether biodiversity would differ if Carp Creek contained only sunny, only shaded, or a patchwork of sunny and shady habitats.

RESULTS

Effect of light intensity on the number of individual within different of macroinvertebrate taxa

Overall, our results suggested that the majority of taxa in this study did not have a preference for sunny vs. shaded habitats. During our first round of sampling, the average abundance of individuals in the sixteen taxa (stonefly, threadworm, caddisfly, water mite, amphipod, midge, crane fly, water snipe fly, beetle, horsefly,

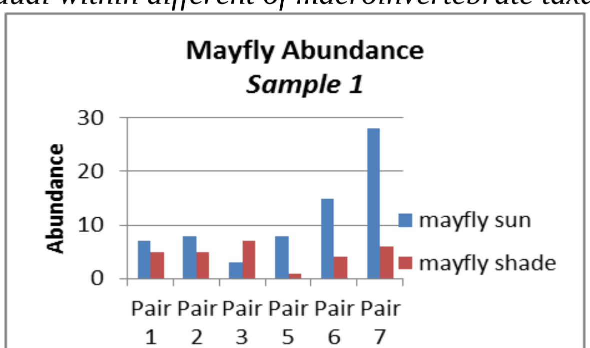


Figure 1. Mayfly abundance (number of individuals) in each of six pairs of sites during

tubifex worm, segmented worm, damselfly, black fly, dance fly, and unidentified) did not differ between sun and shade. However, in our first sampling, 65% more mayflies occurred in sun than shade (7.83 ± 6.04 vs. 1.67 ± 1.51; paired t = 2.75, d.f. = 5, p = 0.04; Figure 1).

In our first and second rounds of sampling combined, amphipods were significantly more abundant in sun than shade, suggesting that this taxon also preferred sun (5.00 ± 2.45 vs. 2.00 ± 1.79; paired t = 3.503, d.f. = 5, p = 0.017; Figure 2). Similarly, significantly more midges occurred in the sun than in the shade, also suggesting a preference for sunny areas (59.33 ± 31.46 vs. 27.67 ± 19.38; paired t = 2.856, d.f. = 5, p = 0.036; Figure 3). Beetles seemed to prefer sun as well, but not as strongly. The difference was nearly significant (0.50 ± 0.548 vs. 0.00 ± 0.00; paired t = 2.236, d.f. = 5, p = 0.076). All other macroinvertebrate taxa were found to have similar abundance in sunny and shaded areas, suggesting a lack of preference for light intensity (Figure 4).

Figure 2. Abundance of Amphipods in combined samples.

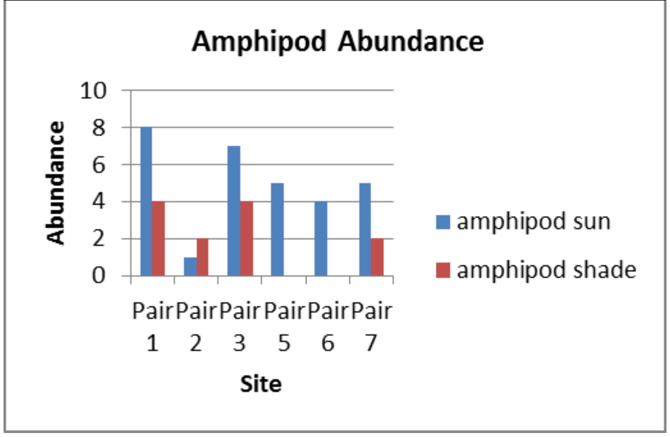
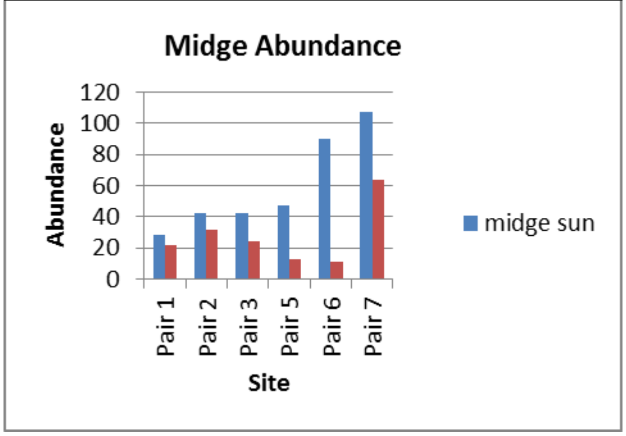


Figure 3. Abundance of Midges in combined samples.



Effect of light intensity on total number of macroinvertebrates

The total number of macroinvertebrates was greater for sun sites than shade sites, suggesting a preference for higher light intensity across all groups. However, the results were only marginally significant (97.0 ± 46.26 vs. 48.33 ± 27.24; paired t = 97.722, d.f. = 5, p = 0.051; Figure 5).

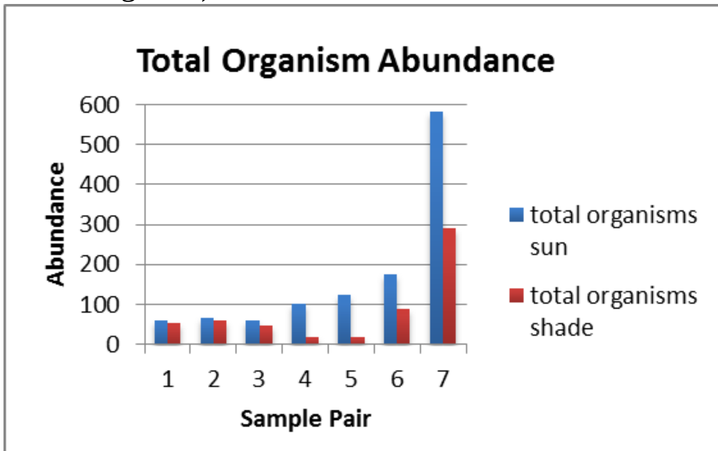


Figure 5. Total number of macroinvertebrates in combined samples.

Effect of light intensity on the total number of macroinvertebrate taxa

In our combined samplings, average number of taxa did not differ significantly between sunny and shaded habitats (8.67 ± 1.97 vs 7.00 ± 2.53; paired t = 1.356, d.f. = 5, p = 0.32). However, four rare taxa were found only in sunny sites (Figure 6). Statistical significance testing was not possible.

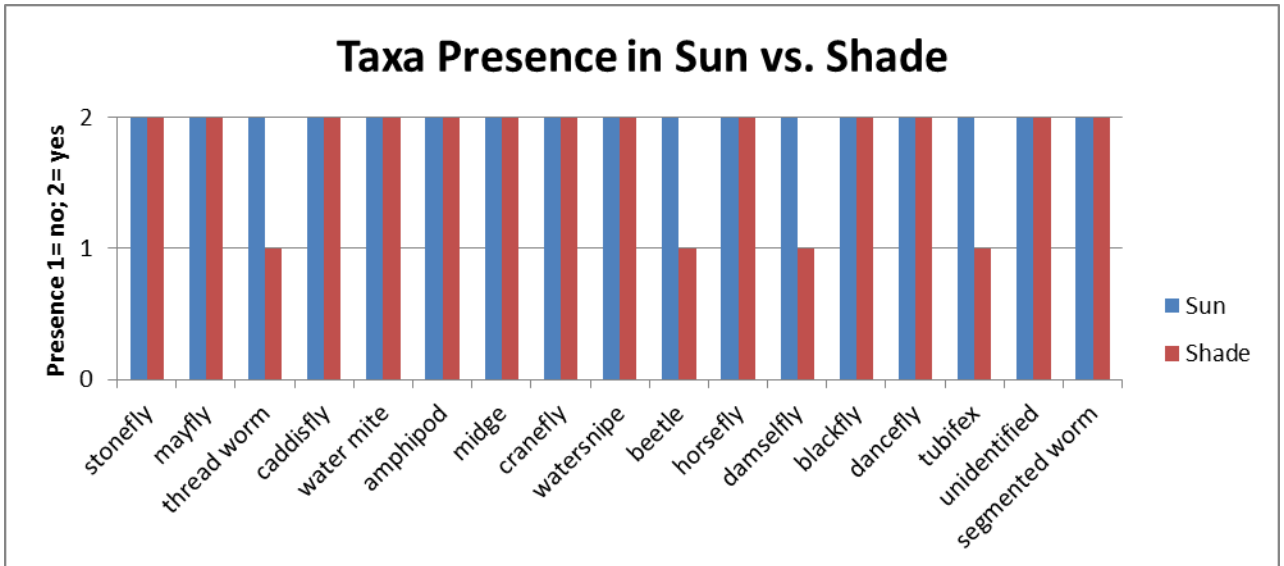


Figure 6. Presence of each taxon in sunny and shaded sites.

Effect of light intensity on overall macroinvertebrate biodiversity

Overall Shannon-Weiner diversity (H') was 1.43 for all sunny sites, 1.54 for all shady sites, and 1.48 for all sunny sites and shady sites combined. This small difference suggests that biodiversity would not differ drastically between hypothetical streams with only sunny sites, only shady sites, or a mixture of sunny and shady sites. Though sunny sites had a greater number of taxa than did shaded sites (Figure 6), the individuals in shaded areas were distributed more evenly among taxa (E_{shade}=0.60, E_{sun}=0.50).

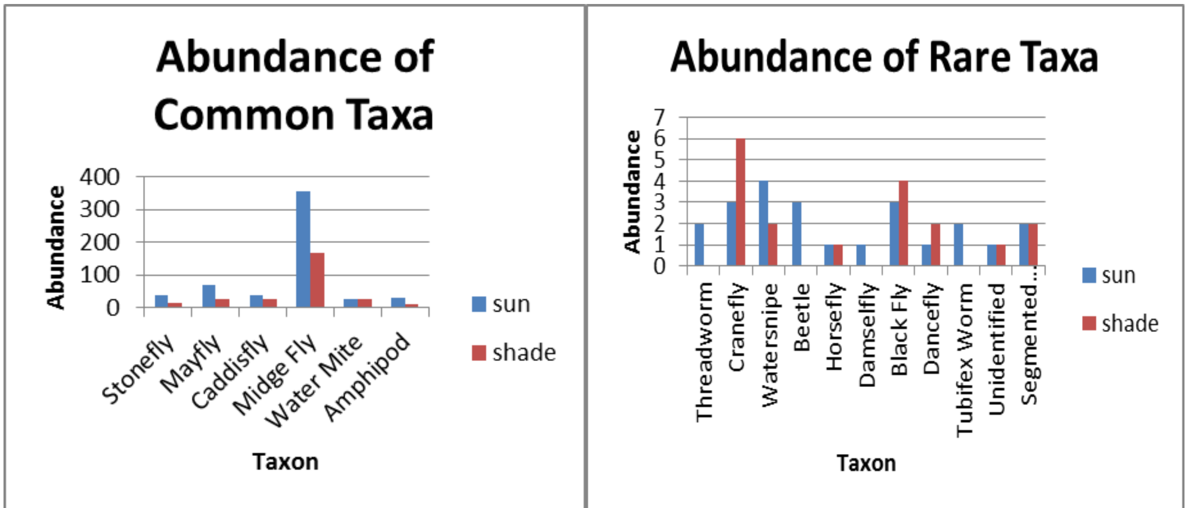


Figure 4. Relative abundances of rare and common taxa across sunlit and shaded areas.

DISCUSSION

Effect of light intensity on average individual abundance of each taxon of macroinvertebrates

Through our sample analysis we found that midges (orders Chironomidae and Ceratopogonidae), mayflies (order Ephemeroptera), and scuds (order Amphipoda) were the only taxa to show significant preference for sun over shade. Due to the non-photosynthetic nature of these organisms, it can be inferred that it is not the amount of sunlight that directly influences the distribution of these taxa, but some other factor that indirectly benefits them. High exposure to sunlight is directly linked with algal growth (Bernhardt & VanderBorgh 1995; Vaughn 1997). If they feed on algae (Voshell 2002), it seems logical that mayflies, midges, and amphipods would prefer to live in sunny areas due to their higher primary productivity (Bernhardt & VanderBorgh 1995).

The higher abundance of midges in our sunny sites is consistent with the findings of Bernhardt and VanderBorgh (1995), who found midge abundances to be significantly linked to higher sunlight in natural and artificial streams. In a study by Vaughn (1997) mayflies both had higher abundances in sun than shade, though the differences were not significant. It is possible that the differences in results between this study and Vaughn (1997) are due to differences in sampling methods – while this study utilized samples taken from substrates in Carp Creek, Vaughn (1997) quantified species found in core samples from the riverbed.

Our observed differences in amphipod abundance were contrary to research about amphipod behavior. In a typical stream environment, higher populations of amphipods have been shown to populate dark, shaded areas, exhibiting negative phototaxis (Voshell 2002). It is this proclivity that generally causes amphipods to be more active at night than during the day (Voshell 2002). The inconsistency found in our data could be explained by a number of confounding factors. Amphipods prefer habitats with rough sediments and materials such as rocks or logs containing crevices in order to hide (Voshell 2002). Smoothness of bark was not standardized among the logs we sampled. If all logs in our sunny sites had rougher bark than those in the shaded sites, the higher amphipod abundance could be due to greater bark roughness rather than to higher sunlight.

Effect of light intensity on average total number of macroinvertebrates

We observed a nearly significantly higher total number of macroinvertebrate individuals in sunny than shaded habitats. More light availability in those habitats may give rise to a more diverse and abundant algal community, due to increased photosynthetic opportunities. A larger concentration of algae may provide more nutrients for macroinvertebrate grazers, because higher light intensity significantly increases algal biomass. It is likely that sunny sites contain food for macroinvertebrates that eat algal matter (Wellnitz & Ward 1998).

It is also possible that macroinvertebrates prefer higher light intensity habitats as a predation avoidance strategy. Since many freshwater fish prey on macroinvertebrates such as fly larvae, it would follow that macroinvertebrates have evolved to avoid their natural predators (Gilinski 1984). In a predator avoidance strategy of their own, most fish prefer to occupy shaded areas because it simultaneously conceals them from above and allows them to see an approaching predator more easily (Helfman 1981). Thus, macroinvertebrates may avoid predation by aggregating in sunny areas where fish are more vulnerable to predation.

In previous studies, macroinvertebrates have been found to prefer sunlight in riverine ecosystems (Vaughn 1997), a finding consistent with our own results. This observation suggests that proactive conservation efforts should focus on increasing the availability of sunlit habitats for macroinvertebrate communities. These organisms may utilize the space for a variety of reasons, including as a food source and as protection from predators.

The difference between sunny and shady sites may have been only marginally significant due to the effect of noisy variables. Although we controlled for depth of substrate from the surface and water velocity, it is possible that these factors had an effect on macroinvertebrate preference for specific habitats and made it difficult to see an existing relationship between light intensity and abundance of organisms. Additionally, it is possible that some fly larvae completed their aquatic life cycles and metamorphosed into terrestrial organisms between sampling days because the samples were taken in the spring. Lastly, the samples may have been inconsistent in size due to human error. Minute changes in water current may have redirected portions of the samples away from nets, thus resulting in some organism loss.

Effect of light intensity on taxa abundance of macroinverebrates

Though the total number of individuals was nearly significantly higher in sunny sites than shaded ones, the average number of taxa did not differ significantly between sunny and shady sites. Together with the observation that most taxa occurred in both sunny and shady sites, this suggests that the two types of sites do not differ significantly in the kind of habitat they provide. While it may be preferable for all organisms to be in sunlight due to higher algal productivity and shelter from predatory fish, the types of algae and substrates available in the two types of sites are likely not different enough to exclude any taxon. An alternative hypothesis is that the motivation to stay in the sun to avoid predatory fish is not a priority in Carp Creek; we noted a surprisingly small number of fish in the stream.

Our results were inconsistent with those of Hawkins et al. (1982), who found a significantly higher number of taxa in sunny creeks than in shaded creeks. This inconsistency could be because our study was conducted in a single river ecosystem, and theirs was conducted in separate rivers. Their study found food type and abundance to be a significant predictor of the presence of certain taxa in different rivers (Hawkins et al. 1982). It is likely that food availability would be relatively consistent within a single stream, like Carp Creek, because of the flow of water from site to site, and therefore not a significant factor in our study. Furthermore, two of their test sites had deciduous forest overhang, while our sites had almost strictly coniferous trees lining the shore.

Though mean taxa abundance did not differ significantly between sunny and shaded sites, there were some rare taxa that were only found in sunny sites. These taxa (threadworm, beetle, damselfly, and tubifex worm) were collected in such low numbers however, (2, 3, 1, and 2, respectively), that it is almost impossible to attribute their absence in shady sites to anything other than the small sample sizes of this study. In the future, we would take a more representative sample with more replicates and larger sample sizes. To determine the reason for the presence (or absence) of taxa in shaded and sunny sites, it would also be helpful to test for the quality, type, and abundance of food, as well as count the number of fish in each site during each sample. Misidentification of taxa due to unfamiliarity of rare taxa could also have accounted for the lack of these taxa in many samples, including shaded sites. Examining correlations between taxa existence and type and abundance of algae would also be helpful in identifying potential causes for the existence and absence of taxa in sunny and shaded sites. Examining correlations between species existence and type and abundance of algae would also be helpful in identifying potential causes for the existence and absence of species in sunny and shaded sites.

Effect of light intensity on overall biodiversity of macroinvertebrates

The final goal of this study was to investigate the potential biodiversity of streams with only sunny sites, only shady sites, or a combination of the two to determine which would maximize diversity of macroinvertebrates. The Shannon-Wiener indices showed little disparity between the three, suggesting that macroinvertebrate biodiversity is not impacted by variation in light intensity. This result is consistent with other studies that highlight water temperature, flow, salinity, depth, and altitude as the environmental factors that create the most pronounced changes in macroinvertebrate community composition in aquatic environments (Piscart *et al*. 2005; Williams *et al*. 2003). Our results were consistent with those of Williams *et al*. (2003), who found that rivers were high in macroinvertebrate diversity and that community composition remained relatively even throughout the river.

It is possible that the small differences in H’ could be caused by the the fact that the biodiversity index is not sensitive to the distinction of rare taxa, thus these rare taxa may have decreased the true measure of biodiversity (Piscart *et al*. 2005). A larger sample size could have produced a more accurate biodiversity rating and would have allowed for stronger statistical analysis with a bootstrapping program. Other means of measuring biodiversity, such as determining the different guilds, could yield more accurate predictions than those based solely on taxa. Therefore, greater efforts are needed to create a clear quantification of macroinvertebrate biodiversity in streams before disregarding light intensity as a potential influence on species distribution and abundance.

CONCLUSION

The initial impetus for the current study was to contribute to knowledge of factors influencing the spatial distribution of macroinvertebrate communities within streams. Such knowledge would help design freshwater conservation strategies by identifying areas of high biodiversity. Since we found little variation in biodiversity, areas of differing light intensities should not be seen as crucial aspects in determining conservation zones for macroinvertebrates. However, it is important to consider other taxa that variation in light intensity may affect when making decisions about whether to preserve or remove overhangs in stream conservation sites.

It may be premature to conclude that a combination of sunny and shady sites would not increase overall stream biodiversity for two reasons. First, the small scale at which the study was conducted may not have reflected the distribution of diversity that could exist in larger patches of sun and shade, and therefore led us to conclude falsely that no real difference exists. Second, if conservation efforts focused solely on sunny or shady conservation and the choice between habitats was removed, biodiversity may decrease. For example, if macroinvertebrates chose sunny spots in order to avoid fish predation, removing shady hideouts for fish would almost inevitably increase predation in the sun. This phenomenon would lead to a lower overall biodiversity, which would demonstrate the importance of patchy habitats that may not have been visible before.

It is important to recognize the limitations of this study; its scope is a single stream in a short time frame with data relating only to macroinvertebrates on one type of substrate. To fully understand the range of biodiversity within lotic ecosystems for conservation strategies and to determine the effect of variation in light intensity on communities, more large-scale studies must be conducted on other organisms. In addition, we suggest more extensive studies on macroinvertebrates in different areas of the stream: the other three sides of a log, other substrates, along the shoreline, and different benthic communities, for example. More extensive data would help to develop comprehensive proactive conservation programs that would maximize biodiversity in freshwater ecosystems.

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Literature Cited

Angelier, E. 2003. Ecology of Streams and Rivers. Science Publishers, Inc., Enfield, NH.

Arthington, A.H., R.J. Naiman, M.E. McClain, and C. Nilsson. 2010. Preserving the biodiversity and ecological services of rivers: new challenges and research opportunities. Freshwater Biology 55:1-16.

Bernhardt E.S. and M. VanderBorgh. 1995. The effects of light intensity of epipelic algae and associated fauna. UMBS REU Project.

Brooks T. M., R.A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, A. S. L. Rodrigues. 2006. Global Biodiversity Conservation Priorities. Science 313:58-61.

Cushing, C.E., and J.D. Allan. 2001. Streams: Their Ecology and Life. Academic Press, San Diego, CA.

ESA. 2000. *Ecosystem Services*. Ecological Society of America, Washington D.C. http://www.esa.org/education_diversity/pdfDocs/ecosystemservices.pdf

Geist, J. 2011. Integrative freshwater ecology and biodiversity conservation. Ecological Indicators 11: 1507-1516.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65: 455-468.

Hawkins, Charles P., Michael L. Murphey, and N.H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63: 1840-1856.

Helfman, G.S. 1981. The advantage to fishes of hovering in shade. Copeia 1981: 392-400.

Kormondy, E.J. 1996. Concepts of Ecology. Prentice Hall. Upper Saddle River, NJ.

Odum, Eugene P. 1971. Fundamentals of Ecology. W.B. Saunders Company, Philadelphia, PA.

Piscart, C., J.C. Moreteau, and J.N. Beisel. 2005. Biodiversity and structure of macroinvertebrate communities along a small permanent salinity gradient (Meurthe River, France). Hydrobiologia 551:227-236.

Strayer, D.L. 2006. Challenges for Freshwater Invertebrate Conservation. Journal of the North American Benthological Society 25: 271-287.

Townsend, C.R. 1980. The Ecology of Streams and Rivers. Edward Arnold Publishers Ltd. Bedford Square, London.

Turner, W.R., K. Brandon, T.M. Brooks, R. Costanza, G. A. B. Fonseca, and R. Portela. 2007. Global Conservation of Biodiversity and Ecosystem Services. BioScience 57:868-873.

Vaughn, L. 1997. Effects of high versus low light irradiance on biomass and abundance of four orders of invertebrates in depositional zones at various sites throughout the East Maple River. UMBS General Ecology.

Voshell, J.R. 2002. A Guide to Common Freshwater Invertebrates of North America. McDonald and Woodward Publishing Company, Blacksburg, VA.

Way, C.M., A.J. Burky, C.R. Bingham, and A.C. Miller. 1995. Substrate Roughness, Velocity Refuges, and Macroinvertebrate Abundance on Artificial Substrates in the Lower Mississippi River. Journal of the North American Benthological Society 14: 510-518.

Wellnitz, T. A. and J. V. Ward.1998. Does light intensity modify the effect mayfly grazers have on periphyton?. Freshwater Biology, 39: 135–149.

Williams, P., M. Whitfield, J. Biggs, S. Bray, G. Fox, P. Nicolet, and D. Sear. 2003. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biological Conservation 115: 329-341.