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Temporal Changes in Temperature May Suggest Microhabitat Shifts in Larval Spongillafly *Climacia areolaris* Hagen (Neuroptera: Sisyridae) Abundance and Density in a Temperate Freshwater Quarry

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Abstract

Abiotic factors such as temperature and depth are known to affect aquatic insect populations and are thought to be major variables that directly impact how communities are assembled and populations distributed. The purpose of this study was to examine the role of temperature and depth in structuring *Climacia areolaris* Hagen (Neuroptera: Sisyridae) populations within a temperate freshwater quarry. Larval densities among individual sponges at different depths were determined over six months in a Pennsylvania quarry. Sponges from four depths (7.0–8.0 m; 8.1–9.0 m; 9.1–10.0 m and 10.1–12.0) were collected once per month (n = 3) using Self-Contained Underwater Breathing Apparatus (SCUBA). Temperature data were collected at four depths (n = 3 samples/depth). Larval densities significantly varied over the study period, but were not significantly different between depths on any date. Mean total larval density was significantly higher in March, April and May compared to dates later in the season. This result followed an inverse pattern where there was a significant effect of date on temperature, but no difference between depths. There was a detectable change in relative abundance of the sisyrid populations among the depths; the two shallowest depth ranges collectively represented > 50% of the population during March and April, but were < 50% throughout the rest of the summer. There was also a significant negative relationship of larval density with temperature. This shift in abundance as a function of depth could be explained by larvae migrating to sponges in shallower depths as they prepare to exit the lake for pupation. Few studies have documented the role of abiotic factors such as depth and temperature on the spatial and temporal structuring of spongillafly microdistribution within a quarry environment.

Keywords: Sisyridae, *Climacia areolaris*, microhabitat distribution, depth, temperature, freshwater quarry

The interaction of abiotic and biotic variables can determine or influence microhabitat selection by aquatic insects. Some variables might affect the distribution of aquatic insects by exerting their influence over a large geographical area although they may be less important when dealing with microhabitats (Rabeni and Minshall 1977). More specifically, numerous abiotic factors that are known to affect aquatic insect population and community structure, but temperature, sunlight and water depth are thought to be primary variables that directly impact how communities are assembled and populations distributed (Sweeney 1984, Steinman et al. 1991). On a broad

scale, temperature is a good predictor of geographical range for many macroinvertebrate species and, at a finer scale, temperature can directly influence metabolism, growth and development, which may affect population density (Huryn and Wallace 2000; Benke and Huryn 2006, 2010). Moreover, sunlight has indirect effects on macroinvertebrate populations by influencing food resource quantity and quality, particularly primary producers (Steinman et al. 1991, Tank et al. 2010). In addition, water depth is a critical factor in maintaining functional stability of natural and anthropogenic lentic aquatic systems such as ponds, lakes and possibly quarries (Nöges and Nöges 1999, Dong et al. 2014, Li

et al. 2017), primarily because deeper water generally results in lower light intensity and higher water pressure but also greater stability of other factors in the aquatic environment, e.g. temperature and sediment (Bonsor et al. 2017). Dunson and Travis (1991) noted that certain abiotic factors and associated physiological tolerances of organisms have been empirically correlated to the ecological functioning of aquatic macroinvertebrates. For example, life histories can be directly shaped in response to environmental stimuli, and understanding such influences is particularly important for understudied aquatic taxa such as spongillafies (Neuroptera: Sisyridae).

Our limited understanding on the biology/ecology of the Sisyridae in North America is mostly documented through new locality records, taxonomical descriptions and geographical distribution studies sporadically conducted through several state and regional studies (Banks 1906, Old 1933, Brown 1952, Parfin 1952, Chandler 1956, Parfin and Gurney 1956, Gurney and Parfin 1959, Isom 1968, Poirrier 1969, Throne 1971, Poirrier and Arceneaux 1972, Brown 1974, Grigarick 1975, Frost 1976, White 1976, Huggins 1980, Poirrier and Holzenthal 1980, Lago 1981, Stoaks et al. 1983, Lawson and McCafferty 1984, Clark 1985, Oswald et al. 2002, Rasmussen and Pescador 2002, Bowles 2006, Murray-Stoker et al. 2018, Rothfuss and Heilveil 2018, Fisher et al. 2019). The handful of studies that have focused on the ecology of Sisyridae have concentrated on the spongillafly/sponge association (Poirrier 1969, Resh 1976, Matteson and Jacobi 1980, Stoaks et al. 1983; Rothfuss and Heilveil 2018, Fisher et al. 2019), life history (Brown 1952, Pupedis 1985, Loru et al. 2007) and feeding ecology (Poirrier and Arceneaux 1972, Skelton 2009). Little attention has focused on the environmental ecology of larval sisyrids in the northeastern United States.

Because of the paucity of information available on the ecology of Sisyridae, specifically, *Climacia areolaris* (Hagen) in the northeastern United States, the purpose of this study was to examine the importance of temperature in structuring *C. areolaris* populations within a temperate freshwater quarry. Our objectives included: 1) characterizing the temperature gradient with depth; 2) documenting the abundance and density of spongillafies with depth and; 3) correlating temperature with insect density as a function of depth. This simple ecological community may provide insight into how temperature may influence microhabitat distributions, food resource availability as well as spongillafly/sponge community dynamics and structure.

Materials and Methods

Study Site. This study was conducted from March–August in a 23 ha spring-fed limestone quarry located in Willow Springs, Pennsylvania in 2002. The quarry has a maximum depth of approximately 16–18 m and is typically used as a recreational site for SCUBA divers and other activities such as camping, swimming and fishing (Fig. 1). Within the quarry are several anthropogenic structures (e.g., automobiles, school buses and small boats/ships) purposely placed at various depths for recreational diving. These structures also serve as substrate (in addition to the quarry floor and walls) for freshwater sponge, *Spongilla* sp.

Physical/Chemical/Sample Data Collection. Sponge samples were collected once per month ($n = 3$) using SCUBA (Self-Contained Underwater Breathing Apparatus) from four depths: 7.0–8.0 m; 8.1–9.0 m; 9.1–10.0 m and 10.1–12.0. The depths were recorded with a SCUBA Pro dive computer and depth gauge on a Mares regulator. Due to air restrictions limiting time underwater, water temperatures were measured at each collection depth using a gauge in the Genesis regulator ($n = 3$ temperature reading/depth) and taken approximately 12–30 meters of each other at the same depth. Sponges were carefully removed with a knife from each depth and placed immediately into individual 250 ml plastic containers. Sponges and associated spongillafies were preserved at the quarry edge with 95% ethanol and returned to the laboratory for identification and enumeration using Merritt et al. (2008) and Frost et al. (2001).

Data Analysis. The effects of time, depth and their interaction on larval densities were analyzed using repeated measures 2-way ANOVA with Bonferroni corrected post-tests. Statistical tests were considered significant at an alpha level of 0.05. Because there was not a significant effect of depth in that analysis, a repeated measures 1-way ANOVA with Bonferroni post-tests was then used to test for differences in total larval densities (larvae from all depths pooled) among sampling dates, and the same analyses were used to test for water temperature differences among different depths and dates. The relationships between larval density and temperature were modeled by simple linear regression. We modeled mean sampling date density and temperature as one analysis, as well as individual samples with their respective temperatures in a second analysis in order to explore the role of depth in larval density variation at each temperature. All data were tested for normality, and density and temperature were log transformed accordingly for matched parametric tests. All



Figure 1. Google map of Willow Springs Quarry in Richland, PA. Arrows indicate locations and approximate depths (A = 7–8m, B = 8.1–9m, C = 9.1–10m, D = 10.1–12m) from where sponges were collected for spongillafly sampling.

analyses were performed using GraphPad Prism 4.0 and 9.0 (Motulsky 2003).

Results

Although other Sisyrid species are found in Pennsylvania, all larvae collected at all depths were *C. areolaris*. Larval densities significantly varied over the 2002 summer, but were not significantly different among depths on any date or interaction between depth and date (Table 1), therefore, larvae among depths were pooled to make between-date comparisons. Mean total larval density was significantly higher ($F = 14.80$; $df = 5$; $P < 0.0001$) in March, April and May compared to dates later in the season (Fig. 2). This finding followed an inverse pattern with significant differences in temperature among months ($F = 130.9$; $d.f. = 5$; $P < 0.0001$), but no difference among depths sponges were collected ($F = 1.84$; $df = 3$; $P = 0.05$) (Fig. 3). Zoochlorellae were observed in the sponges but not quantified in this study.

Even though no statistical difference was found in larval density among depths, there was a detectable change in relative abundance of the populations among the depths (Fig. 4); the two shallowest depth

ranges collectively represented > 50% of the population during March and April, but were < 50% throughout the rest of the summer. When individual samples were plotted with their respective temperatures there was a significantly negative relationship of larval density with temperature (Fig. 5).

Discussion

Aquatic insect assemblages and their geographical distributions may be structured by several interacting biotic and abiotic factors such as predator/prey relationships, thermal variability as well as food availability (Anderson et al. 2019, Verberk et al. 2020). The majority of studies published to date have documented geographical distributions for *C. areolaris* and other sisyrids and several studies have documented abiotic influences on freshwater sponge distribution and population dynamics (Rader 1984, Lauer et al. 2001, Barnes and Lauer 2003, Fisher et al. 2019); however, of the limited number of ecological treatises on larval spongillafies, this is the only study that has documented the role of abiotic factors such as depth and temperature on the spatial/temporal struc-

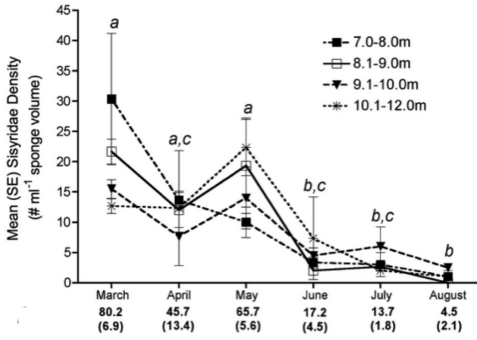


Figure 2. Mean (SE) *Climacia areolaris* density per volume of sponge at four depth ranges over the 2002 summer in Willow Springs Park Quarry, Richland, PA.

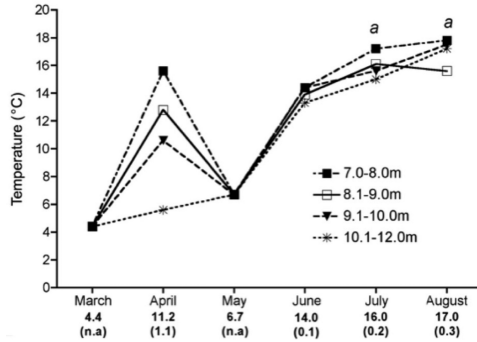


Figure 3. Water temperatures measured at each depth range during sponge collections. For each depth there were three measurements recorded, but there was no variation within a depth range, thus, there are no error bars for each depth. For both graphs the sampling date mean is given in bold along the x-axis, and matching letters above the data points indicate no significant difference in means on that date using Bonferroni post-tests.

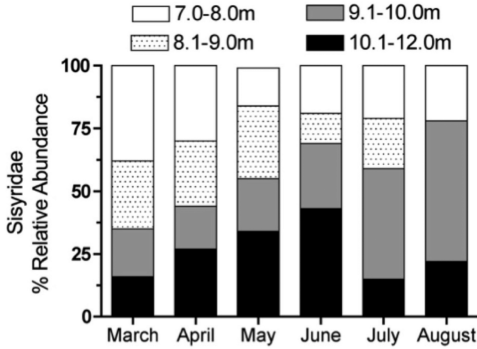


Figure 4. *Climacia areolaris* percent relative abundance of habitat at four depth ranges over the 2002 summer in Willow Springs Park Quarry, Richland, PA

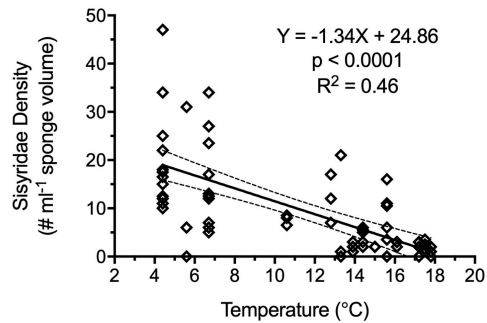


Figure 5. Individual sponge sample density of *Climacia areolaris* and associated temperature measurement for the 2002 summer in Willow Springs Park Quarry, Richland, PA, indicating depth variation of *C. areolaris* density at similar temperatures.

turing i.e., a temporal microdistribution of larval spongillafly populations.

Spongillafies can be found in both lentic (e.g., ponds and lakes) and lotic systems (e.g., streams) (Murray-Stoker et al. 2018). Because these systems differ considerably in their physical and chemical attributes, inherently, the biology of Sisyridae populations found in lentic versus lotic systems may possibly be different. Murray-Stoker et al. (2018) documented spatial distributions across wetland systems over a temporal scale. In our study, we found that the spatial distribution was vertically oriented as a function of depth within our study system in that *C. areolaris* were observed between 7–12 m between March and August in a quarry, and that a reduction of larval relative abundance was strongly correlated with temperature over time as larvae migrated

towards shallower depths prior to the initiation of pupation. This depth shift in relative abundance was associated with temperature profiles throughout the summer (Fig. 4, 5), but this is explained by the population dynamics related to larval migration for emergence during the later part of the summer. Brown (1952) indicated that while on the sponge, larvae tend to remain calmly feeding along side siblings, but he did not mention any kind of movement by spongillafies from one sponge to another or one depth to another prior to pupation. Water temperatures in May did not reflect the warming trend observed at the lower depths. With spring storms, this period may have exhibited high

Table 1: Summary statistics for the repeated measures 2-way ANOVA performed with sampling date and depth as factors. Bonferroni post-tests for multiple comparisons were employed to test for between depth and between date differences (see Table S1).

Source of Variation	Df	Sum-of-squares	Mean Square	F	% of total variation	P-value
Interaction	15	934.4	62.3	1.45	13.39	0.170
Date	5	3563.0	712.6	16.63	51.05	< 0.0001
Depth	3	33.0	11.0	0.12	0.47	0.946

Table S1: Bonferroni post-test results for multiple comparisons that were done after the repeated measures 2-way ANOVA with date and depth as factors.

Bonferroni's multiple comparisons test	Mean Diff.	95.00% CI of diff.	Significant?	Summary
March				
8.1-9.0m vs. 7.0-8.0m	-8.667	-28.46 to 11.13	No	ns
9.1-10.0m vs. 7.0-8.0m	-14.83	-34.63 to 4.961	No	ns
10.1-12.0m vs. 7.0-8.0m	-17.67	-37.46 to 2.128	No	ns
9.1-10.0m vs. 8.1-9.0m	-6.167	-25.96 to 13.63	No	ns
10.1-12.0m vs. 8.1-9.0m	-9	-28.79 to 10.79	No	ns
10.1-12.0m vs. 9.1-10.0m	-2.833	-22.63 to 16.96	No	ns
April				
8.1-9.0m vs. 7.0-8.0m	-1.667	-21.46 to 18.13	No	ns
9.1-10.0m vs. 7.0-8.0m	-6	-25.79 to 13.79	No	ns
10.1-12.0m vs. 7.0-8.0m	-1.333	-21.13 to 18.46	No	ns
9.1-10.0m vs. 8.1-9.0m	-4.333	-24.13 to 15.46	No	ns
10.1-12.0m vs. 8.1-9.0m	0.3333	-19.46 to 20.13	No	ns
10.1-12.0m vs. 9.1-10.0m	4.667	-15.13 to 24.46	No	ns
May				
8.1-9.0m vs. 7.0-8.0m	9.333	-10.46 to 29.13	No	ns
9.1-10.0m vs. 7.0-8.0m	4	-15.79 to 23.79	No	ns
10.1-12.0m vs. 7.0-8.0m	12.33	-7.461 to 32.13	No	ns
9.1-10.0m vs. 8.1-9.0m	-5.333	-25.13 to 14.46	No	ns
10.1-12.0m vs. 8.1-9.0m	3	-16.79 to 22.79	No	ns
10.1-12.0m vs. 9.1-10.0m	8.333	-11.46 to 28.13	No	ns
June				
8.1-9.0m vs. 7.0-8.0m	-1.333	-21.13 to 18.46	No	ns
9.1-10.0m vs. 7.0-8.0m	1.167	-18.63 to 20.96	No	ns
10.1-12.0m vs. 7.0-8.0m	4	-15.79 to 23.79	No	ns
9.1-10.0m vs. 8.1-9.0m	2.5	-17.29 to 22.29	No	ns
10.1-12.0m vs. 8.1-9.0m	5.333	-14.46 to 25.13	No	ns
10.1-12.0m vs. 9.1-10.0m	2.833	-16.96 to 22.63	No	ns
July				
8.1-9.0m vs. 7.0-8.0m	-0.3333	-20.13 to 19.46	No	ns
9.1-10.0m vs. 7.0-8.0m	3	-16.79 to 22.79	No	ns
10.1-12.0m vs. 7.0-8.0m	-1	-20.79 to 18.79	No	ns
9.1-10.0m vs. 8.1-9.0m	3.333	-16.46 to 23.13	No	ns
10.1-12.0m vs. 8.1-9.0m	-0.6667	-20.46 to 19.13	No	ns
10.1-12.0m vs. 9.1-10.0m	-4	-23.79 to 15.79	No	ns
August				
8.1-9.0m vs. 7.0-8.0m	-1	-20.79 to 18.79	No	ns
9.1-10.0m vs. 7.0-8.0m	1.5	-18.29 to 21.29	No	ns
10.1-12.0m vs. 7.0-8.0m	0	-19.79 to 19.79	No	ns
9.1-10.0m vs. 8.1-9.0m	2.5	-17.29 to 22.29	No	ns
10.1-12.0m vs. 8.1-9.0m	1	-18.79 to 20.79	No	ns
10.1-12.0m vs. 9.1-10.0m	-1.5	-21.29 to 18.29	No	ns

winds associated with storm events and the resultant effect on the quarry temperature was cooling due to the associated mixing of deeper cooler waters with warmer shallower waters (Singleton et al. 2013). Spongillafly densities responded with greater numbers collected from shallower depths (e.g., more *C. areolaris* were observed between 8.1–9.0 compared to 9.1–10 meters). However, there are several reasons this finding may be an artifact of a low sample size ($n = 3$), the lake is highly regulated in terms of diver use and natural history sampling. In order to not deplete sponge populations on the various structures over an entire year, we limited the harvest number to three sponges. Because of this limitation and others related to SCUBA access and time to dive the quarry for sampling, we would recommend a greater number of sponges sampled to better understand the relationship between depth and water temperature.

The close evolutionary history shared between host (sponge) and predator (spongillafly) is diverse and complex (Farrell et al. 2021). Spongillafly typically feed on the algal symbionts within these sponges, their mouthpart morphology is adapted to piercing and sucking algal cells from within the sponge matrix (Merritt et al. 2008) as well as on the bryozoan cells (Cover and Bogan 2015). Unfortunately, we did not quantify zoochlorellae in the sponges however, because spongillafly feed primarily on zoochlorellae in sponges (Skelton and Strand 2013), perhaps the seasonality we observed in *C. areolaris* relative abundance and density is partially explained through its close association with the host sponge and algal food resource and movement among depths may be an effort to maximize growth and development with respect to optimally foraging on the algal symbionts.

Season and temperature are known to influence freshwater sponge distribution, biomass and productivity (Harsha et al. 1983, Melão and Rocha 1988). Anecdotally, we noticed lower total sponge densities over time along with increasing water temperatures and shifts in relative abundance into colder waters indicating a temperature relationship with larval densities. We observed a temporal shift in depths with significantly more spongillafly being collected from sponges at shallow depths during the warmer months compared to more at deeper depths (Fig. 3). One explanation for this shift to shallow, warmer waters may be explained by food abundance and availability being greater at these depths due to the effect of light availability on algal growth and reproduction in shallow, warmer waters (Sand-Jensen and Pedersen 1994). An alternative explanation for this temporal shift among depths may

be a behavior employed to select optimal respiratory requirements moving towards colder climates where dissolved oxygen levels will be higher (Croijmans et al. 2021). In addition, freshwater sponges can grow in shaded, deeper waters if adequate suitable food particles are present (Sand-Jensen and Pedersen 1994). Therefore, since spongillafly will feed on both zoochlorellae as well as sponge cells (Skelton and Strand 2013), it is feasible that the respective abundance shifts of spongillafly to colder waters may be an indicator of sponge abundance, health and productivity (Gugel 2001). To address how temperature may affect sponge growth and size, future work will focus on the temporal effects on sponge life history in temperate lakes as a function of depth and temperature.

Some metacommunity models describe patch dynamics, mass effect, species sorting and neutral effects for understanding how community structure may be influenced by spatial dynamics (Ellis et al. 2006). The spongillafly-sponge model may provide a worthy testing ground for such models. Moreover, it would allow researchers to address a rarely examined aspect of sponge/spongillafly population dynamics, i.e., the role of spatial synchronicity in their community structure as driven by such exogenous (abiotic) factors as temperature. Complex spatial dynamics related to overall species productivity and distribution may well be as common as spatial synchrony in natural systems (Liebhold et al. 2004). While evolutionary and ecological dynamical processes may drive the niche partitioning for spongillafly and their host sponges, the quest to understand the mechanisms behind spatio-temporal dynamics of spongillafly on sponge patches may be dependent on our ability to differentiate if spongillafly production and distribution are by chance or driven by competition for limited resources (Bonsall et al. 2004).

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