Cutthroat Trout as a Despotic Competitor in Pool Habitat

Josef Mayor

1122 NE Boat St, Seattle, WA 98105

mayorj@uw.edu

ABSTRACT

Habitats can provide organisms a fitness advantage through the environmental conditions and resources it provides. When organisms compete to occupy the habitat of the highest quality, there can be competitive inequalities that allow one species, the despotic competitor, to force others out into lower quality habitats. Due to their relatively large size, aggressively competitive nature, and preference for pools, cutthroat trout in Rock Creek may serve as a despotic competitor in the pool habitat. To test this idea, I compared biodiversity of pools with and without cutthroat trout, *Oncorhynchus clarkii*, as well as the relationship between cutthroat length and biodiversity, to determine if cutthroat trout act as a despotic predator and if their competitive ability increases with size. I found that biodiversity was significantly ($p < .04$) lower in pools with cutthroat trout and that length had no significant ($p > .16$) impact on the biodiversity. This implies that cutthroat do act as despotic competitor in the pool habitat as their presence lowers the quality of the habitat and forces individuals of other species into different habitats. Such an understanding of the Rock Creek community could prove crucial with the potential threat of invasion from non-native brook trout, *Salvelinus fontinalis*. These brook trout traditionally outcompete cutthroat and could force them out of their role as a despotic competitor, upsetting the current community structure and shifting species distributions.

Keywords: competition, stream, Rock Creek, biodiversity

INTRODUCTION

The quality of the habitat that an organism occupies can strongly influence the fitness of the individual. To succeed and reproduce, an organism's habitat must align with its niche: the environmental conditions which allow a species to survive and reproduce (Hutchinson 1957). Suitable habitat will have all the resources an organism needs throughout its life history including food, appropriate climate conditions, and breeding opportunities. The more closely a given habitat aligns with that organism's niche, the more suitable the habitat is and the greater the fitness advantage it can provide (Pulliam 2000).

Given the inherent fitness advantages of occupying ideal habitat and the variability in available habitat quality, organisms experience intraspecific and interspecific competition for the most advantageous habitats. If among the competing individuals there exists no phenotypic diversity and no competitive advantage, then the community fits to an ideal free distribution (Fretwell 1969). In such a distribution, the most suitable habitat experiences the highest density of individuals while the remaining habitats experience progressively lesser densities relating to their lesser suitability (Krebs 1985). In effect, it becomes progressively more advantageous for organisms to take up less suitable habitat as the competition in the ideal habitat stiffens, exploiting all available resources and filling all available niches. As a result, the individuals distribute to the different habitats in densities proportional to the quality of the habitat. Such distributions shift when competitive inequality exists among the individuals and species vying for a given habitat. The strongest competitors reap the benefits of occupying the most suitable habitat with progressively weaker competitors occupying progressively less suitable habitat (Parker and Sutherland 1986). Those strong competitors lower the density of individuals in the most desirable habitat because their presence and competition lower the quality of that habitat for other species. In even more extreme circumstances, an exceptionally territorial and strong competitor species can command an ideal habitat, preventing the presence of other species; such a distribution is referred to as an ideal despotic distribution (Fretwell 1969). Controlling the most suitable habitat gives the despotic competitor exclusive access to the superior resources, relegating other species to inferior habitats.

Pool habitats in streams have several characteristics which could make them the most suitable habitat for a wide variety of species. For one, the deeper water of the pools protect from aerial and terrestrial predators (Lonzarich and Quinn 1995). The deeper waters also provide the shelter of cooler temperatures that many species rely on, particularly during the summer months (Matthews and Berg 1997). The slower moving waters found in pools also require less effort from the organism to navigate in or to hold their position, improving energy efficiency (Rosenfeld and Boss 2001). Pool habitats are often the locations of greatest abundance or diversity in stream environments (Langeani et al. 2005, Lonzarich and Quinn 1995). Such diversity would align with an ideal free distribution in which no one species has a competitive advantage for controlling the pool allowing all to congregate in most suitable habitat. However, if a despotic competitor in a stream ecosystem preferred the pool as its most suitable habitat, it could force out the other species and displace them into other, less-suitable habitats.

Cutthroat trout, *Oncorhynchus clarkii,* have characteristics which could make them a despotic competitor for pool habitat in stream ecosystems. Cutthroat display a preference for pool habitats at all ages, with the preference becoming a requirement at larger sizes (Rosenfeld and Boss 2001, Mesa 1991). Such a requirement for survival would create a significant selective pressure for cutthroat to strongly compete or dominate in pool habitats to ensure their presence there. Cutthroat display aggressive behavior to defend their feeding area or occupied habitat

(Seiler and Keeley 2007). Such aggressive behavior could allow cutthroat to deter other species from occupying pool habitat, creating an ideal despotic distribution in the stream environment.

This study investigated the potential of cutthroat trout as a despotic competitor by analyzing the distribution of the fish community in the Rock Creek, Washington ecosystem. If cutthroat act as a despotic competitor in Rock Creek, then the biodiversity of pools with cutthroat should be lower than pools without because the cutthroat outcompete and force out individuals of other species, forcing them to occupy less preferable habitats.

METHODS

Study Site

Rock Creek is a tributary for the Cedar River, which flows into Lake Washington. A dam exists on the Cedar River downstream of the Rock Creek confluence. In 2003, a fish passage addition to the dam allowed for fish to move upstream of the dam and into tributaries such as Rock Creek to spawn ("Rock Creek" n.d.). Allowing anadromous species to return to spawning grounds should have increased the biodiversity of Rock Creek, strengthening the analysis of this study by reintroducing species which could directly compete with cutthroat such as Coho salmon, *Oncorhynchus kisutch*.

Data

The students of the Fish 312 course collected data on the fish community within Rock Creek from 2003 to 2019. The data set includes counts and sizes of aquatic individuals observed in the selected reaches of the stream for each year. Pool and riffle habitat units were sampled at each of three sites along the length of the stream: a lower, middle, and upper reach. In each habitat for each reach, fish abundances were recorded using a backpack electro fisher. For each caught fish, the students recorded species, length, and age if possible. They also noted the depth, velocity, substrate size, and distance to the bank of the stream location the fish was found. Habitat measurements were taken in 1-meter increments across with transect of the stream with 4 meters between each transect. At each point, water velocity, depth, and substrate size were recorded to provide an understanding of the size and conditions of each habitat.

Statistical Analysis

In order to determine the role of cutthroat trout as despotic competitors, we compared biodiversity in pools with cutthroat against pools without cutthroat. The Shannon Index (H′) served as a measure of biodiversity in the analysis:

$$H' = \Sigma [-P_i * (\ln P_i)] \qquad (1)$$

The Shannon index is based around the term P_i), the proportion of species “i” in the assemblage of species. The index reflects both species richness and evenness (“Week 1” n.d.). Cutthroat were not included in the calculation for biodiversity in pools where they were present, as the index was used to assess the effect of cutthroat on other species. Including cutthroat would have artificially raised the biodiversity index when comparing to pool where they were not present.

All statistical tests will use a p value of .05 as the cutoff for significance. A T-test will determine if there exists a difference in Shannon Index between pools with cutthroat and pools without cutthroat. Linear regression tests analyzing the relationship between cutthroat size in the pool and biodiversity in the pool should provide further insight as to whether the size of cutthroat present affects local biodiversity and therefore whether they act as a despotic competitor.

RESULTS

Biodiversity Comparison

The biodiversity indices of pools with cutthroat trout were lower in pools than those of pools without cutthroat trout. The pools without cutthroat had a significantly higher biodiversity ($p \approx .037$) than those with (FIG.1). This analysis operated with 76 degrees of freedom, resulting in a t statistic of -1.81. Further investigation including the biodiversities of all habitats, pools and riffles, in the analysis of habitat with cutthroat versus habitat without cutthroat yielded an insignificant result ($p \approx .052$) (FIG.2). Across all habitats there were 13 unique species observed: Chinook salmon, Coho salmon, crayfish, cutthroat trout, lamprey, newt, pacific giant salamander, rainbow trout, reticulate sculpin, speckled dace, tailed frog tadpole, torrent sculpin, trout.

Cutthroat Length Impact

The length of cutthroat in the pools had no effect on the biodiversity index. Regression analysis did not find a significant relationship between biodiversity and maximum ($p > .16$) or average ($p > .19$) length of cutthroat in the pool (FIG. 3 and FIG. 4). The data also fit poorly to the trend lines with the maximum and average plots returning r^2 values of .042 and .037 respectively.

DISCUSSION

Pool habitats in Rock Creek had significantly lower biodiversity when cutthroat trout were present, implying that the trout act as a despotic competitor and lower the quality of the habitat for other species. As a strong competitor, the cutthroat would be able to more effectively control or use the resources of the pool, which leaves less opportunity for other species. For some of those species, a reduction of habitat quality as a result of cutthroat presence may force them into other habitats, such as riffles, even if those alternate habitats would not usually be as suitable as a pool. The fact that the trend of cutthroat presence lowering biodiversity did not hold up when including both pools and riffles in the analysis suggests several potential mechanisms. It is possible that this is a reflection of the cutthroat preference for pools. With the strong cutthroat competitors controlling the pools, the weaker cutthroat would likely have a negligible effect on biodiversity in their less preferred riffle habitat. It could also be due to a different despotic competitor which controls riffle biodiversity or some other factor which makes the impact of cutthroat on riffle biodiversity negligible.

The idea of cutthroat trout being strong competitors in the stream environment is not unprecedented. For example, cutthroat outcompete Coho salmon, a species found in Rock creek, with greater foraging success and more aggressive behavior, consistently chasing their counterparts (Sabo and Pauley 1997). In a pool, such aggressive behavior would allow cutthroat to exclude potential competitors and their foraging success would limit the food available to other species.

My analysis found no relationship between maximum or average cutthroat length in the pool and the biodiversity of the pool. This would imply that for Rock Creek, the size of the cutthroat is unconnected to their strength as a competitor and effect on other species. This would contradict previous work which has found that the competitive ability of cutthroat trout increases with the size of the fish (Sabo and Pauley 1997). However, it could also be that size was not important in the Rock Creek environment because there is a notable absence of other large salmonids. The previous work has largely focused on cutthroat's competitive interactions with salmonids of similar size, so it is possible that in Rock Creek, most of the cutthroat are large enough to act as a despotic competitor because of the lack of an equally sized aggressor (Sabo and Pauley 1997).

Though my conclusions seem to indicate that cutthroat of most sizes act as despotic competitors in Rock Creek pools, there could be alternate explanations for my findings. For one, the pools the cutthroat are dominating could be unique habitats unsuitable for some other species. The biodiversity of pools with cutthroat could be lower because the habitat cutthroat prefer is of lower quality for some other species and individuals. Understanding this potential relationship will require further analysis of the habitat data with comparisons of habitat with and without cutthroat trout. It is also possible that the cutthroat does not serve as a despotic competitor for the whole community but rather for a few specific species which they directly impact or prey upon. Understanding this potential relationship will require further analysis of species present with and without cutthroat to determine which are affected by the trout presence.

While cutthroat may currently control the species occupying pools in Rock creek, the introduction of non-native species could complicate that system. Though perhaps dominant in Rock Creek, cutthroat struggle to compete against other more aggressive salmonids and often get relegated to less preferable habitat in their presence (Hawkins 1997). Specifically, non-native brook trout, *Salvelinus fontinalis,* pose a significant threat to cutthroat as a superior competitor, capable of rapidly increasing their abundance within novel habitat (Peterson et al. 2004). Despite brook trout not directly interfering with cutthroat feeding, their presence has been found to cause cutthroat populations to decline (McGrath and Jr 2007). Among the potential explanations for this trend is behavioral aggression between the two species, which could cause cutthroat to take up sub-optimal habitat, resulting in population declines (McGrath and Jr 2007). When present, brook trout act as a despotic competitor which reduces habitat quality for cutthroat likely through the same behavioral aggression which makes cutthroat despotic competitors in Rock creek. Understanding the role of cutthroat in stream communities of the Pacific Northwest will be crucial to understanding potential of invasion from new despotic competitors, such as brook trout.

Overall, Rock Creek pool habitats exhibit an ideal despotic distribution with cutthroat serving as the dominant competitor. Their presence prevents species from occupying the pool habitat by lowering the habitat quality for those other species, likely through behavioral aggression and superior foraging on finite prey resources. The potential introduction of a competitor for cutthroat, brook trout, could cause a decline or redistribution of cutthroat which would change the community dynamics of Rock Creek. Any decline or redistribution which prevents cutthroat from so effectively defending pools would open up previously blocked niches in the desirable pool habitat. While the habitat quality for cutthroat may decline, brook trout could cause a habitat quality increase or decrease for other species, resulting in a restructuring of the Rock Creek community.

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REFERENCES

Fretwell, S. D. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:45–52.

Hawkins, D. 1997. The effects of interspecific interactions and hybridization on coastal cutthroat trout. Sea-run cutthroat trout: biology, management, and future conservation.

Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Krebs, C. J. 1985. Review of Ecology: The Experimental Analysis of Distribution and Abundance. Beta Beta Beta Biological Society.

Langeani, F., L. Casatti, H. S. Gameiro, A. B. do Carmo, and D. de C. Rossa-Feres. 2005. Riffle and pool fish communities in a large stream of southeastern Brazil. Neotropical Ichthyology 3:305–311.

Lonzarich, D. G., and T. P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. Canadian Journal of Zoology-Revue Canadienne De Zoologie 73:2223–2230.

Matthews, K. R., and N. H. Berg. 1997. Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. Journal of Fish Biology 50:50–67.

McGrath, C. C., and W. M. L. Jr. 2007. Competition and Predation as Mechanisms for Displacement of Greenback Cutthroat Trout by Brook Trout. Transactions of the American Fisheries Society 136:1381–1392.

Mesa, M. 1991. Variation in Feeding, Aggression, and Position Choice Between Hatchery and Wild Cutthroat Trout in an Artificial Stream. Transactions of the American Fisheries Society 120:723–727.

Parker, G. A., and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Animal Behaviour 34:1222–1242.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population Ecology of an Invasion: Effects of Brook Trout on Native Cutthroat Trout. Ecological Applications 14:754–772.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Rock Creek. (n.d.). . Lab Lecture, Fish 312 Course Materials.

Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58:585–593.

Sabo, J. L., and G. B. Pauley. 1997. Competition between stream-dwelling cutthroat trout (Oncorhynchus clarki) and coho salmon (Oncorhynchus kisutch): effects of relative size and population origin. Canadian Journal of Fisheries and Aquatic Sciences 54:2609–2617.

Seiler, S. M., and E. R. Keeley. 2007. A comparison of aggressive and foraging behaviour between juvenile cutthroat trout, rainbow trout and F1 hybrids. Animal Behaviour 74:1805–1812.

Week 1. (n.d.). . Fish 312 Course Materials.

Figure captions.

Fig. 1. Shannon diversity index for pools without cutthroat ($n=31$) and pools with cutthroat ($n=47$). Biodiversity significantly greater for pools without cutthroat ($p < .04$).

Fig. 2. Shannon diversity index for pools and riffles without cutthroat ($n=50$) and pools and riffles without with cutthroat ($n=105$). No significant ($p > .05$) difference in biodiversity.

Fig. 3. Maximum length of cutthroat in pool versus Shannon biodiversity index of that pool. No significant ($p > .16$) relationship.

Fig. 4. Average length of cutthroat in pool versus Shannon biodiversity index of that pool. No significant ($p > .19$) relationship.

Fig. 1.

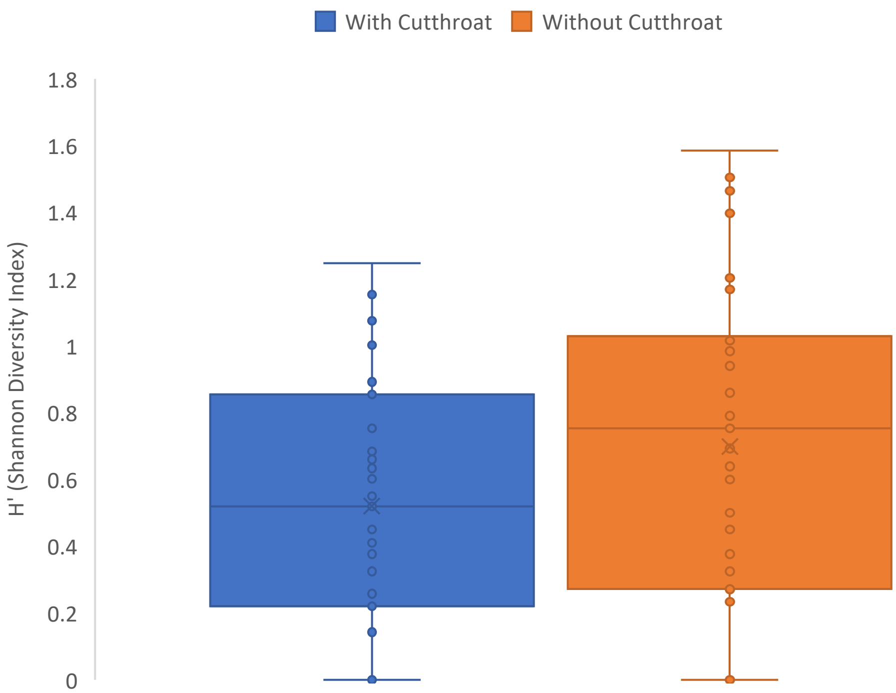

With Cutthroat
Without Cutthroat
H' (Shannon Diversity Index)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0

Fig. 2.

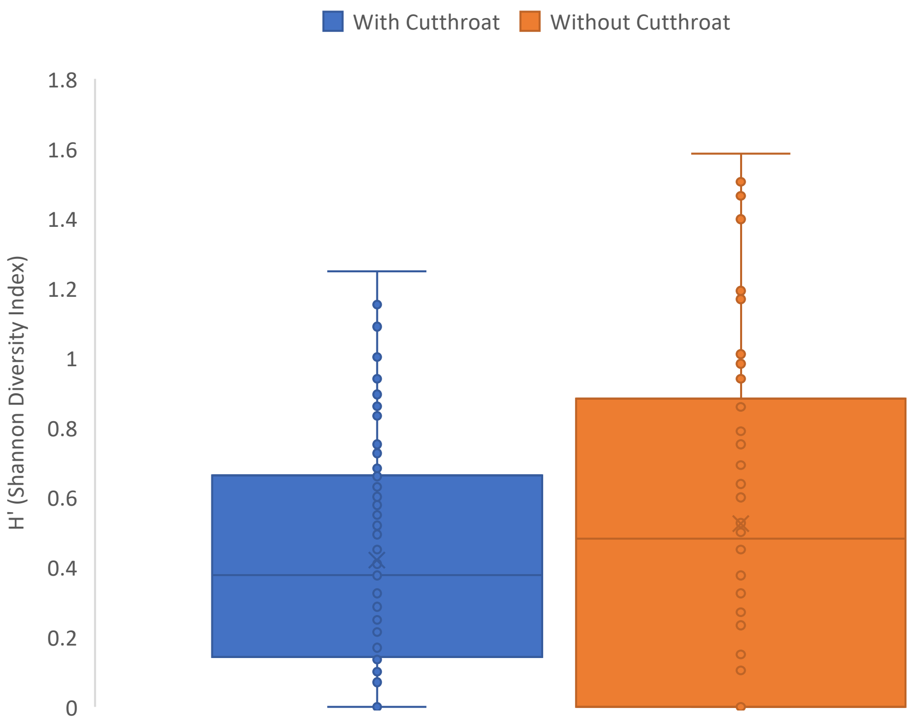

With Cutthroat
Without Cutthroat
H' (Shannon Diversity Index)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0

Fig. 3.

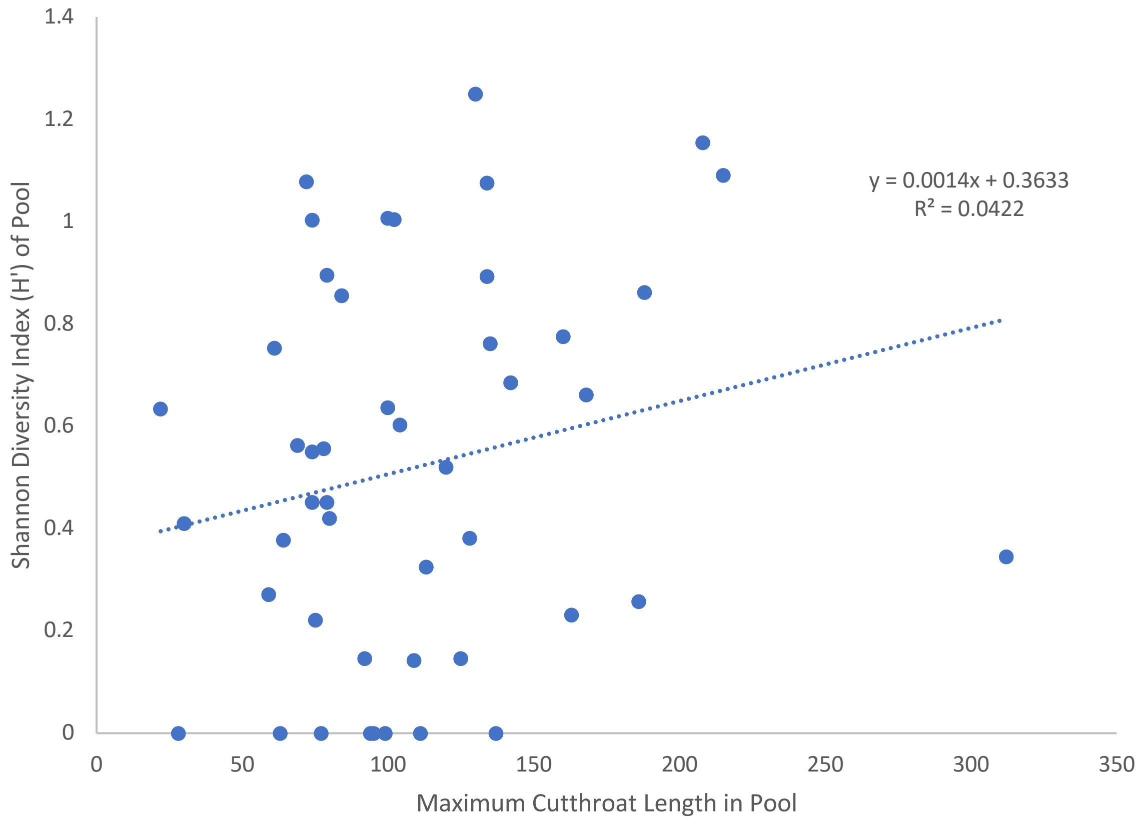
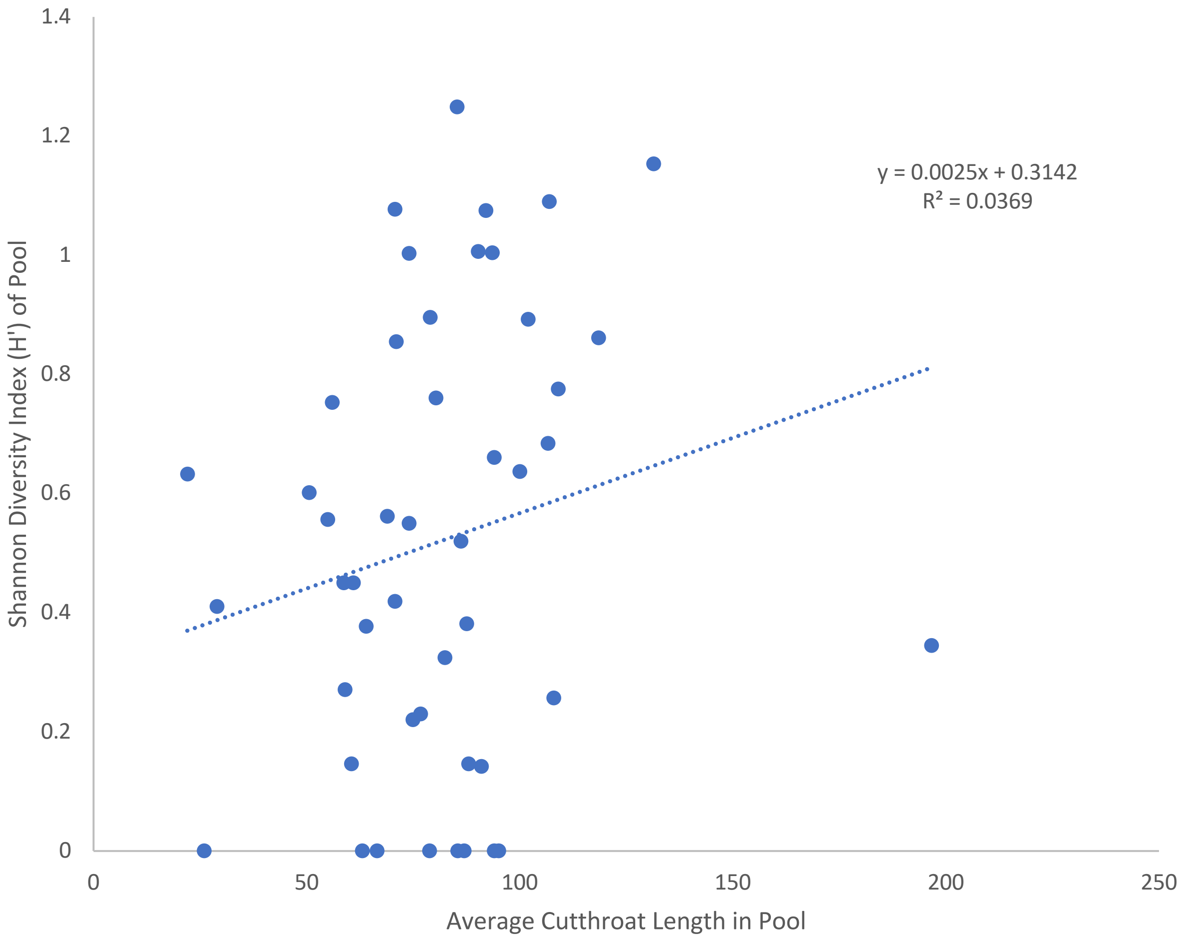

y = 0.0014x + 0.3633
R² = 0.0422
Shannon Diversity Index (H') of Pool
Maximum Cutthroat Length in Pool
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
50
100
150
200
250
300
350

Fig. 4.


1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
50
100
150
200
250
Shannon Diversity Index (H') of Pool
Average Cutthroat Length in Pool
y = 0.0025x + 0.3142
R² = 0.0369