

Effects of light availability and source lake DOC concentration on Bluegill (*Lepomis macrochirus*) foraging habits

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Abstract

Dissolved organic carbon (DOC) in lakes has been shown to influence the foraging habits of visual predators. DOC concentrations have been rising in recent years, and continued increases are predicted due to environmental change. Because fish foraging significantly impacts zooplankton communities, changes in fish feeding habits can have cascading effects on food web interactions. I investigated the effects of source lake DOC concentration and light availability on the feeding behavior of Bluegill (*Lepomis macrochirus*). I hypothesized that Bluegill would forage better under high light availability, and under the light conditions corresponding to their source lake. Additionally, I expected there to be size selectivity for smaller zooplankton in dark water for both light and dark adapted fish. Feeding trials were performed with juvenile Bluegill from both high and low source lake DOC and under high and low light availability. The overall proportion of zooplankton consumed in each trial was not affected by source lake DOC or light availability, but selectivity for smaller zooplankton under lower light availability was found for fish from the low DOC source lake. The zooplankton used in feeding trials were very different from the zooplankton community in the high DOC source lake, which may have impacted the results. Determining how fish foraging behavior might change under future DOC increases can help predict the effects on food chains these changes may have.

Introduction

The amount of dissolved organic carbon (DOC) in a lake is an important control on ecosystem structure. Originating from terrestrial plant material, organic carbon is modified in the soil by microorganisms and minerals, and transported to lakes by groundwater and surface water (Solomon et al. 2015). DOC concentration affects the structure of lakes, particularly the thickness of the surface layer, or epilimnion. Because DOC absorbs light, an increase in DOC concentration creates a darker, and therefore, thinner epilimnetic environment. Reducing the depth of the epilimnion means that there is less primary production as a result of less light availability. In addition, darker lakes are colder, which causes decreased metabolic rates in aquatic organisms (Fee et al. 1996). Environmental variables such as pH, temperature, and hydrological processes can affect DOC concentration, and previous studies have shown increases in DOC concentrations across Europe and North America over the last ten years. Climate change

is a possible cause of these increases, and climate change is predicted to cause increases in DOC in the future (Evans et al. 2005).

Increased DOC can negatively impact the foraging success of fish. Changes in water color have been shown to severely impact the feeding efficiency of common Eurasian perch (*Perca fluviatilis*). When feeding trials were performed in highly humic and clear water, perch consumed significantly more plankton in the latter and it was argued that decreased visibility in darker water had a negative impact on visual predators' abilities to hunt prey (Estlander et al. 2012). In addition, Bluegill (*Lepomis macrochirus*) exhibited decreased feeding on zooplankton under higher levels of DOC during feeding trials (Weidel et al. 2017).

Increased DOC can also affect size selectivity of planktivorous fish, causing fish to consume smaller sizes of zooplankton than they would under higher light availability. The contrast degradation theory states that when particles, such as DOC, absorb or scatter light, the visibility of objects decreases exponentially with distance. Therefore, it has been suggested that size selectivity for smaller zooplankton by Bluegill will occur under higher DOC concentrations (De Robertis et al. 2013). Increased turbidity has been shown to reduce the reactive distance of Bluegill to zooplankton, and the effect was even stronger for larger sizes of zooplankton, which is in support of the contrast degradation theory (Vinyard and O'Brien 2011). In contrast, Gardner (2011) found size selectivity to be independent of turbidity in feeding trials using Bluegill and two size classes of *Daphnia*.

Eco-Evolutionary dynamics may play a role in Bluegill foraging in different light climates. These dynamics occur when ecological change causes phenotypic change in an organism which can result in ecological change. An example of an Eco-Evo feedback is when fish evolve to feed more efficiently on zooplankton and in turn, the zooplankton evolve to better

avoid predation and the cycle continues (Hendry 2016). A second example of an Eco-Evo feedback involves genetic variation in guppies (*Poecilia reticulata*). Guppies adapted to either high or low predation affected the biomass of the aquatic invertebrates that the guppies preyed on (Pelletier et al. 2009). As such, increased concentrations of DOC may be influencing Bluegill foraging where Bluegill become more efficient foragers under the light climate they inhabit (phenotypic response) and can ultimately, modify the zooplankton community (environmental response). Further, DOC concentration may influence the zooplankton community of a lake, indirectly affecting fish foraging. Studies have been performed to determine the effects of acclimation to light and dark water on feeding efficiency. Stasko et al. (2015) found that the feeding behavior of dark-adapted fish were less impacted than the feeding behavior of light-adapted fish in response to changes in water clarity, although this relationship was weak. Eco-evo feedbacks may be present in this particular system if the light climate Bluegill are adapted to affects their foraging behavior. Finally, differences in zooplankton community composition may influence fish foraging in addition to physical components such as light climate.

Given that temperate lakes are darkening and darker lakes have been shown to alter foraging behavior of fish, I investigated the effects of DOC concentration on feeding behavior in juvenile Bluegill. By performing feeding trials under high and low light availability using Bluegill with high or low source lake DOC concentrations, I considered whether acclimation to a particular light climate affects feeding behavior. This can help predict how future changes in DOC concentration might influence food chains in lakes by showing how fish might adapt if DOC concentrations continue to rise. If light adapted fish can't forage as well as dark adapted fish under higher DOC concentrations, the consequences of future DOC increases on light lakes will be more drastic than expected if only dark adapted fish were used to make predictions. I

hypothesized, overall, that Bluegill would forage better in under high light availability. Further, I hypothesized that Bluegill would forage better in the light conditions corresponding to the light climate they originated from. Additionally, due to the contrast degradation theory, I expected there to be size selectivity for smaller zooplankton in dark water for both light and dark adapted fish.

Methods

Fish Collection

Juvenile Bluegill ranging from 60-80 mm in length were caught using minnow traps in two lakes on the property of University of Notre Dame's Environmental Research Center (UNDERC). Fish were removed from the traps and placed in tanks to acclimate 24 hours before trials. The dark-adapted Bluegill were caught in Hummingbird Lake (HB) while the light-adapted Bluegill were caught in Crampton Lake (CR). DOC concentration (mg/L) and color (g440) were used to determine light climate of each lake (Table 1).

Feeding Trials

Three trials were performed for HB and CR Bluegill in both high and low light availability for a total of 12 trials. Cattle tanks were filled with filtered lake water taken from Tenderfoot Lake on the property of UNDERC to represent high light availability. To induce dark water conditions for low light availability, Super Hume, a brown commercial dye, was added to Tenderfoot water. The amount of Super Hume added to each tank was determined by taking light intensity ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) measurements in the tanks using a Li-Cor LI-250A light meter and adding dye until the tank conditions matched light profiles taken from HB. Zooplankton collected from Tenderfoot Lake using an 80 μm mesh zooplankton tow was added to each tank and served as the food source. An additional tow was taken each day that a trial was conducted

and was subsequently preserved and counted to determine the initial zooplankton density and relative amounts of taxa. A total of ten fish were placed in a tank for each trial and starved for 24 hours. Fish were allowed to feed for two hours after which they were euthanized using tricaine methanesulfonate (MS-222). To determine foraging success and size selectivity, gut contents were dissected, identified and counted according to the methods put forth by Weidel et al (2017).

Statistical Analysis

Foraging success was measured by determining the proportion of zooplankton consumed out of the total number of zooplankton added to a tank. The proportion consumed of each individual zooplankton taxa was calculated as well. In addition, the relative proportions of large (*Daphnia*, Chaoborus, Calanoida) and small (Bosmina, Cyclopoida) zooplankton found in each fish stomach were quantified. Small and large size classes of zooplankton were determined using Brooks and Dodson (1965). The number of empty stomachs from each trial was recorded. R statistical software was used to perform two-way ANOVAs, followed by Tukey post-hoc tests on the overall proportion of zooplankton consumed in the trials, and on the proportions of specific zooplankton taxa consumed with source lake DOC concentration and light availability as factors.

Results

No statistically significant differences were found in overall proportion of zooplankton added to a tank that were consumed between HB and CR Bluegill (ANOVA $p=0.848$) or between high and low light availabilities (ANOVA $p=0.393$), and no interaction was found (ANOVA $p=0.395$). Bluegill consumed very small amounts of the total zooplankton, with proportion of zooplankton eaten ranging from 0.0005 to 0.008. (Figure 1). An average of 37% of HB fish and 48% of CR fish ate nothing during the trials (Figure 2).

Zooplankton categorized into small and large size classes suggests fish consumed different sized zooplankton under different treatments. CR fish showed a strong preference for large zooplankton under high light availability, but consumed nearly equal amounts of large and small zooplankton under low light availability. HB fish showed a preference for large zooplankton under high light availability, but this preference was not as pronounced as it was for fish from CR. Under low light availability, HB fish showed a preference for smaller zooplankton (Figure 3).

A two-way ANOVA performed on the average proportion of cyclopoids consumed by Bluegill during feeding trials revealed no significant effects from source lake DOC concentration ($p=0.1964$) or light availability ($p=0.1889$), however a significant interaction was found ($p=0.0317$), showing lower Cyclopoid consumption by Bluegill from HB under higher light availability ($p=0.0697$) and higher Cyclopoid consumption under low light by Bluegill from HB than Bluegill from CR ($p=0.0724$) The proportion of total Cyclopoids consumed ranged from 0.0002 to 0.0175 (Figure 4).

Further, the average proportion of *Bosmina* consumed by Bluegill during feeding trials was examined. In two tanks, no *Bosmina* were eaten, while the maximum *Bosmina* proportion consumed was 0.090. DOC concentration (ANOVA $p=0.6418$) and light availability (ANOVA $p=0.0933$) were not statistically significant in *Bosmina* consumption, however a significant interaction was found (ANOVA $p=0.0499$), showing significant increases in *Bosmina* feeding by CR Bluegill under lower light availability ($p=0.051$) (Figure 5).

A two-way ANOVA revealed significant effects on *Daphnia* consumption from source lake DOC concentration ($p=0.0117$) and light availability ($p=0.0339$), as well as a significant

interaction ($p=0.0450$). Proportions of *Daphnia* consumed ranged from 0 to 0.0077. Overall, the average proportion of *Daphnia* consumed, 0.0213, was the highest out of all the zooplankton taxa. CR Bluegill consumed more *Daphnia* under high light availability, while HB Bluegill fed on more daphnia under low light availability (Figure 6).

Proportions of total Calanoids consumed during trials were examined, and no statistically significant differences were found between high and low source lake DOC (ANOVA $p=0.997$), or high and low light availability (ANOVA $p=0.153$). There was no statistically significant interaction between source lake DOC and light availability (ANOVA $p=0.222$) Proportion of Calanoids consumed ranged from 0 to 0.00465 (Figure 7).

Discussion

Neither source lake DOC concentration nor light availability significantly affected the overall proportion of zooplankton consumed, suggesting that Bluegill are not highly specialized to forage in a particular light environment. Source lake DOC concentration and light availability did, however, affect the selectivity of Bluegill for different sized prey. The optimal foraging theory describes the tendency of predators to consume prey that will provide the greatest energetic benefit to the predator relative to the energetic expense of catching and consuming the prey (Pyke et al. 1977). A study on Bluegill size selectivity corroborates this theory as Bluegill were shown to favor larger size classes of *Daphnia* (Werner and Hall 1974). According to the contrast degradation theory, a decrease in light availability (i.e. scattering of light by DOC) causes larger prey to be less visible than smaller prey, and therefore, water with high DOC concentration is likely to be associated with selection for smaller prey (De Robertis 2003). My data supports the idea that changes in DOC concentration alter the foraging habits of fish, but how these habits are altered depends on the DOC concentration that fish are acclimated to.

CR fish tended to eat larger zooplankton under higher light availability, which is in support of the size selectivity hypothesis. CR fish consumed greater proportions of *Bosmina*, a small zooplankton, under low light and consumed greater proportions of the larger *Daphnia* under high light. HB fish did not consistently follow this pattern, consuming larger proportions of small Cyclopoids under lower light, but smaller proportions of large *Daphnia* under higher light. HB fish had a greater proportion of empty stomachs and could be a result of an altered zooplankton community. Bluegill may be acclimated to the zooplankton communities in their source lakes, and utilizing zooplankton from a lake that the fish did not naturally inhabit could justify why HB fish foraging was not what I hypothesized. Zooplankton tow data collected by a peer showed that the CR zooplankton community was relatively similar to the Tenderfoot zooplankton community that the fish were fed. The HB zooplankton community, in contrast, was different than the Tenderfoot community. The majority of zooplankton counted from HB were *Holopedium* and *Chaoborus*, which were minority taxa in Tenderfoot. Fish reduce the natural populations of the zooplankton that they preferentially feed on (Lynch 1979), so the presence of a greater amount of larger zooplankton in Hummingbird Lake suggests that HB fish prefer smaller zooplankton.

Larval fish can significantly reduce populations of zooplankton. A previous study in a Midwestern lake found that as larval fish densities peaked, zooplankton biomass declined, and when larval fish density declined, zooplankton populations stabilized again (Welker et al. 1994). As lake DOC concentrations continue to rise, the cascading effects Bluegill foraging has on zooplankton may become more pronounced. Because Bluegill are visual feeders, increased feeding on smaller zooplankton under high DOC might shift the zooplankton community to larger sizes. Further, increased DOC may alter trophic relationships because visual feeders will

be affected more than filter feeders. For example, the gizzard shad (*Dorosoma cepedianum*) and Bluegill both feed on zooplankton, and largemouth bass (*Micropterus salmoides*) feed on Bluegill (Stein et al. 1995). Gizzard shad are filter feeders, however, so increased DOC concentrations will have a stronger impact on Bluegill foraging success. This could allow gizzard shad to outcompete Bluegill for zooplankton, decreasing Bluegill populations, and potentially reducing bass populations.

In addition to zooplankton community differences, the size of fish utilized may have influenced the results. Devries and Stein (1992) found that smaller Bluegill prefer smaller zooplankton. Additionally, Li et al. (1985) found that selectivity for larger zooplankton increased with fish size due to better vision in larger fish. The juvenile Bluegill used in this experiment may have been selecting for small zooplankton because they were of smaller size and their vision less developed. Future experiments could investigate the feeding behavior of adult Bluegill, which would perhaps show stronger trends for smaller size selectivity in darker water. Also, performing feeding trials with zooplankton assemblages from multiple lakes could show if Bluegill are acclimated to the zooplankton found in their native lake.

As environmental change increases DOC concentration in lakes, fish foraging will likely be affected. Changes in fish foraging can have significant implications for food webs, because fish can modify zooplankton communities, and zooplankton communities affect the predators that feed on them. Results from future experiments along with the results from my trials can help determine how fish foraging behavior might change under future DOC increases, and the effects on food chains this foraging behavior changes may have, which is important because trophic cascades could affect populations of larger fish. Fishing is important economically, for both

recreation and as a food source, and an understanding of foraging behavior is important for managing Bluegill populations.

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Tables**Table 1.** DOC concentration and color, which is another measurement used to determine lake light climate, of the two lakes where fish were originated from.

Lake	DOC (mg/L)	Color (g440)
Crampton	4.7	1.43
Hummingbird	20.5	19.74

Figures

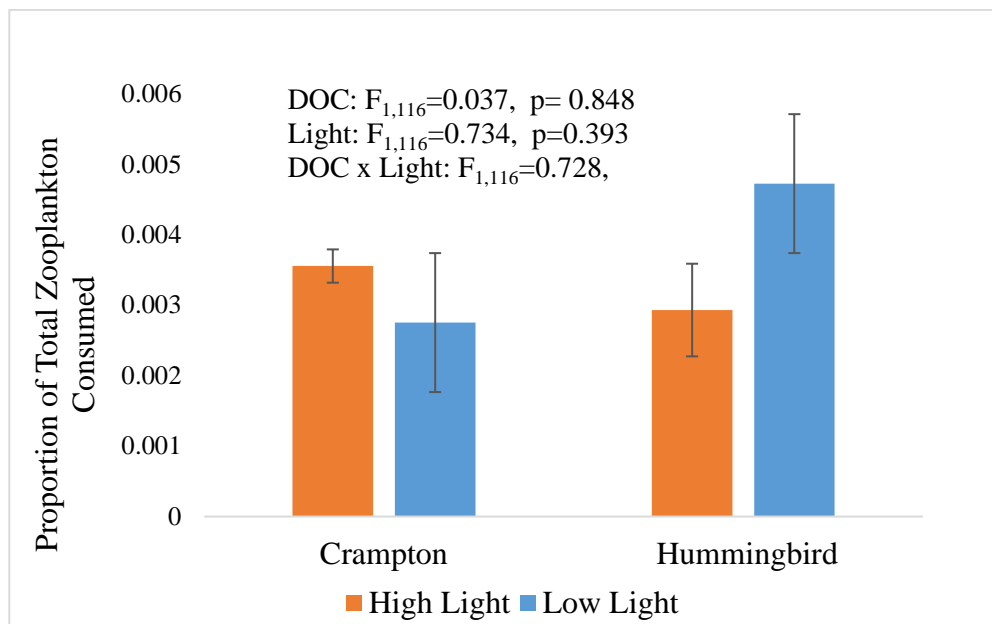


Figure 1: Average proportion (+/- SE) of total zooplankton added to a tank consumed by Bluegill during feeding trials. A two-way ANOVA found no statistically significant differences in overall foraging by bluegill from high DOC and low DOC lakes under high and low light availability.

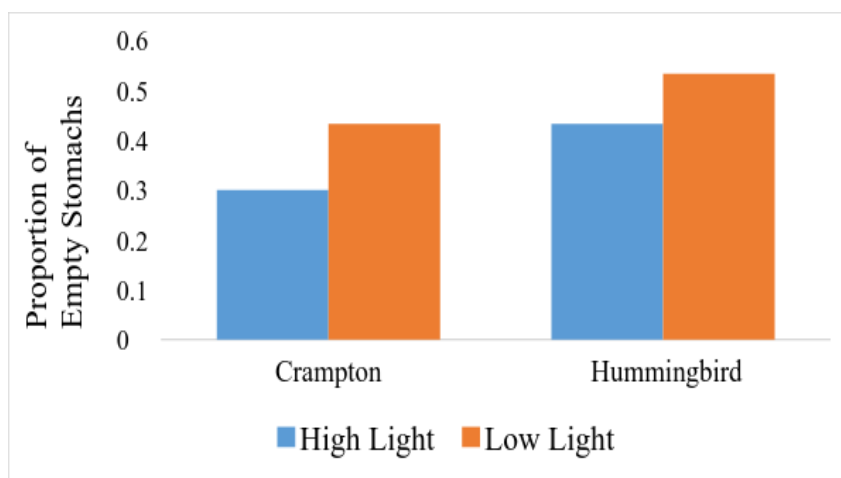


Figure 2: Proportion of Bluegill in each treatment that did not consume anything during feeding trials.

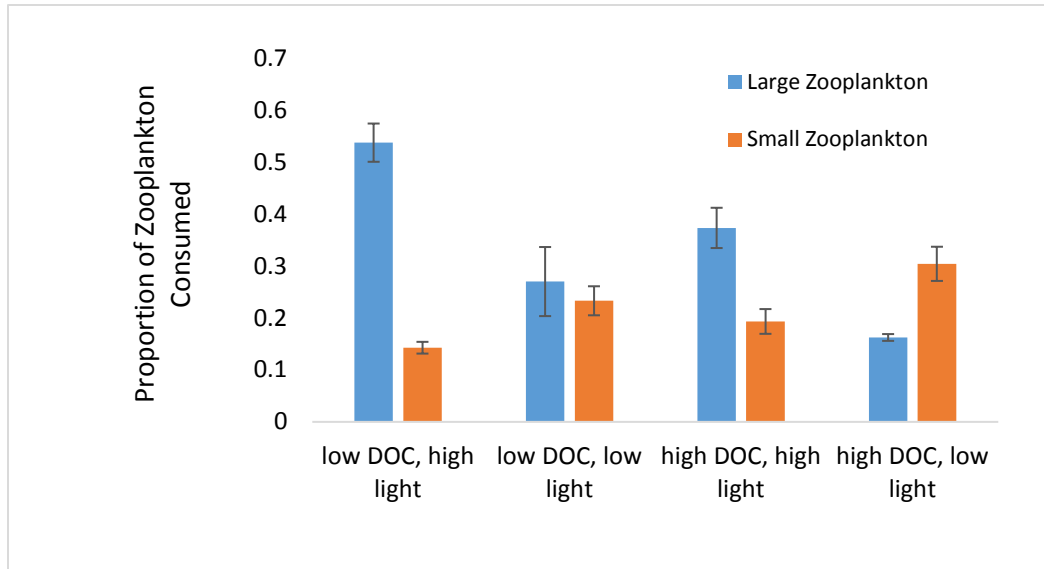


Figure 3: Size Selectivity (+/- SE) of bluegill from high DOC and low DOC lakes, under high and low light availability. Proportions were determined by dividing the number consumed of large zooplankton (*Daphnia*, Calanoid, and Chaoborus) and small zooplankton (*Bosmina*, Cyclopoid) by the total number of zooplankton consumed by an individual fish.

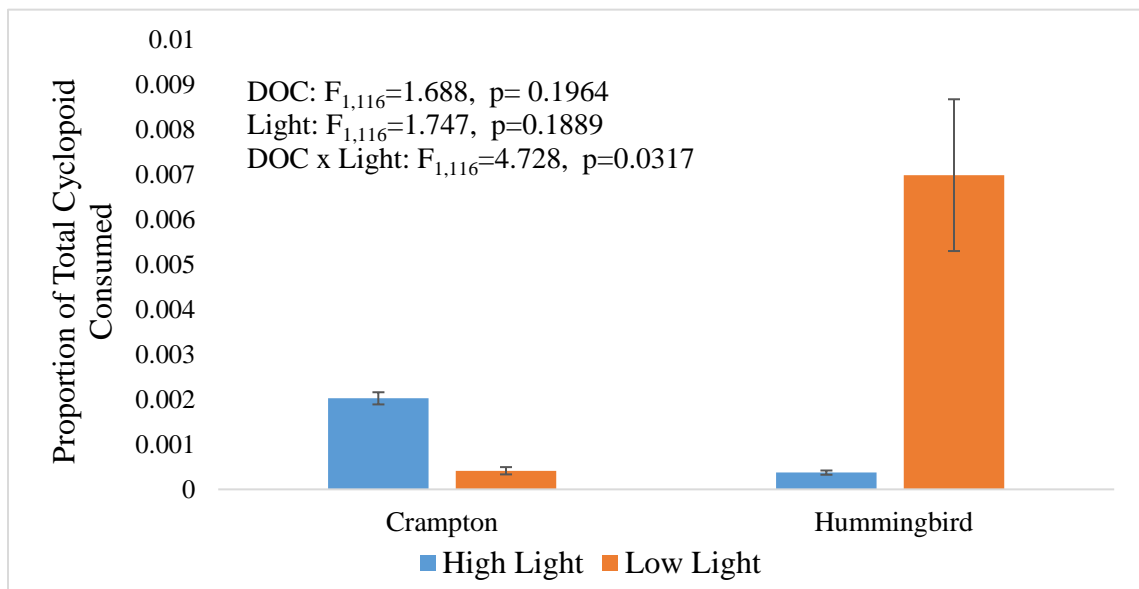


Figure 4: Average proportion of total Cyclopoids consumed by Bluegill during feeding trials (+/- SE), determined by dividing the amount of Cyclopoids consumed by the total amount of Cyclopoids added to a tank.

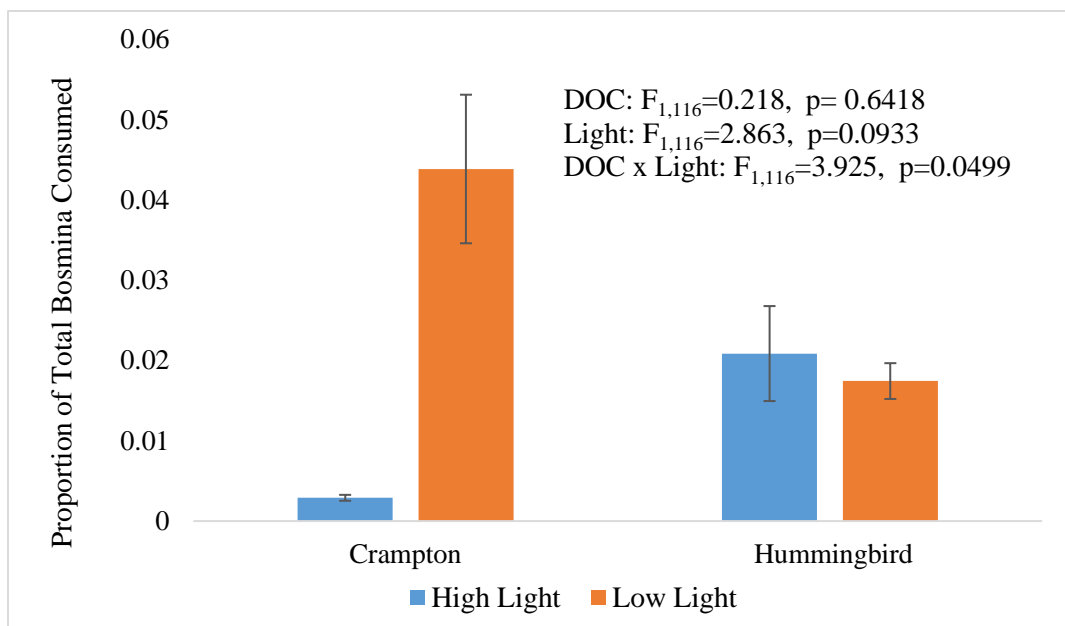


Figure 5: Average proportion of total *Bosmina* consumed by bluegill during feeding trials (+/- SE), determined by dividing the amount of *Bosmina* consumed by the total amount of *Bosmina* added to a tank.

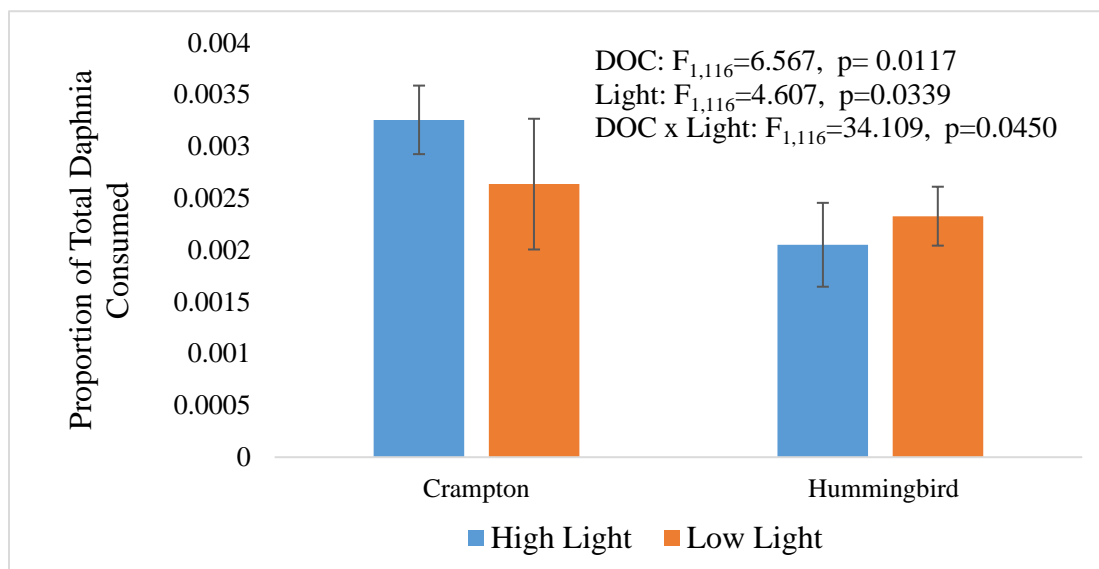


Figure 6: Average proportion of total *Daphnia* consumed (+/- SE) by Bluegill during feeding trials, determined by dividing the amount of *Daphnia* consumed by the total amount of *Daphnia* added to a tank.

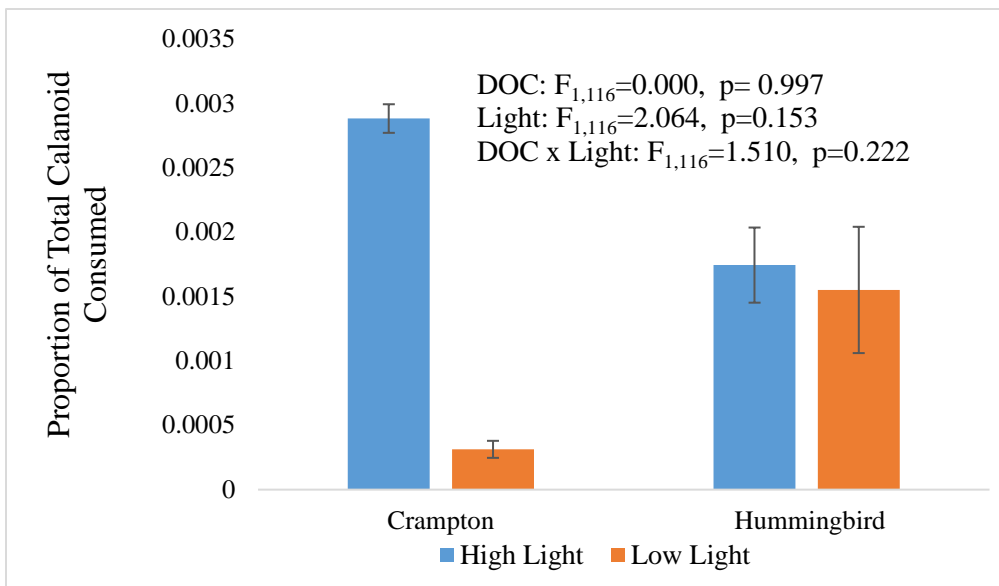


Figure 7: Average proportion of total Calanoids consumed (+/- SE) by bluegill during feeding trials, determined by dividing the amount of Calanoids consumed by the total amount of Calanoids added to a tank.