

Placement and Displacement of *Chaoborus* Larvae in Water Columns Across a Dissolved Organic Carbon Gradient

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Abstract

Dissolved organic carbon (DOC) is an important abiotic factor that absorbs light entering aquatic systems. DOC has been steadily increasing in freshwater systems over the past several decades, and much of that increase can be traced to human effects. *Chaoborus* spp. larvae are integral parts of aquatic food webs and can have large impacts on community structures. They are also a food source for fish and because of this, often exhibit Diel Vertical Migration (DVM). In this study, 3 lakes of differing DOC concentrations at the University of Notre Dame Environmental Research Center (UNDERC), Roach Lake, Long Lake, and Hummingbird Lake, were sampled for chaoborids to examine their placement and movement across a DOC gradient. Chaoborids were found relatively closer to the surface in lakes with higher concentrations of DOC. The relative depth of the average *Chaoborus* was significantly shallower in the high DOC lake than both the medium DOC lake ($p=0.02$) and the low DOC lake ($p<0.0001$). These results suggest a possible cascade effect that could occur in the community structure within lakes with high DOC, decreasing overall fish abundance and diversity which could then adversely influence recreational fishing.

Introduction

Dissolved organic matter (DOM) comes in a variety of forms in lake ecosystems, each of which impacts its ecosystems differently. Dissolved organic carbon (DOC) is an example of a type of DOM and its concentrations in natural waters varies widely from <1 to >50 mg L⁻¹ (Evans et al 2004). The main source of DOC in freshwater systems is leeching of decomposed organic matter from soils and there has been a steady increase of DOC in freshwaters over the past few decades (Sucker and Krause 2009). Some of the increase of DOC can be attributed to human activities. For instance, recent increases in atmospheric carbon dioxide, much of which can be linked to humans, is suggested to increase lentic DOC by stimulating primary plant production which elevates CO₂ levels in the soil which can then be leached into the water (Sucker and Krause 2009). The refractory components present in allochthonous DOC have significant effects on both physical and chemical processes as well as ecosystem structure (Christensen et al. 1997) For instance, DOC has been shown to influence light and temperature levels by absorbing solar radiation, affect the transport and availability of heavy metals, and

control the pH in waters with low-alkalinity (Stanley et al. 2011). These impacts of DOC can directly or indirectly influence the behavior of organisms within lakes.

Chaoborus spp. are an important part of aquatic food webs and are, therefore, greatly significant to freshwater ecosystems they inhabit. Apart from fish, the *Chaoborus* spp. larvae are often the most common planktivore in lakes and can dramatically alter zooplankton communities (Liljendahl-Nurminen 2006; Stratton and Kesler 2011). When fish are not present, the predation by *Chaoborus* has been observed to reduce the density of zooplankton (Arnott and Vanni 1993). Some populations of *Chaoborus* spp. exhibit diel vertical migration (DVM), which refers to the behavior of staying in deep water during daytime hours and rising during nighttime hours in order to feed under the safety of darkness (Wissel et al. 2003; Liljendahl-Nurminen 2006; Stratton and Kessler 2011). This behavior is dictated by chemical cues given off by fish predators, and by remaining in low-light areas during the day (deeper water) they are able to avoid predation more effectively since fish predators rely primarily on vision to capture their prey (Stratton and Kessler 2011).

I am interested in examining impacts of DOC levels on the placement and displacement patterns of *Chaoborus* spp. larvae in several different lakes at the University of Notre Dame Environmental Research Center (UNDERC) in Land O' Lakes, Wisconsin. The three lakes I will use to examine these impacts are Roach Lake (Figure 1), Long Lake (Figure 2) and Hummingbird Lake (Figure 3), which are low, medium, and high DOC lakes, respectively. Since DOC lowers lake light levels by absorbing solar radiation, lakes with higher concentrations of DOC should have lower amounts of light penetrating the water. As noted earlier, predatory fish rely heavily on vision to capture their prey, so I would expect fewer fish in the lower levels of light since they would have more difficulty finding their prey in this condition. Furthermore,

fish, unlike chaoborids, can't survive in hypoxic zones (Wissel et al. 2003), which tend to also have lower levels of light. Since the chemicals from these fish are part of what cue *Chaoborus* spp. larvae to migrate, there may also be more *Chaoborus* spp. when there are fewer predatory fish because of the low light. I hypothesize that *Chaoborus* spp. larvae will be found closer to the surface of the water in the high DOC lake than the medium DOC lake and larvae in the medium DOC lake will be found closer to the surface than in the low DOC lake during daylight and for the difference in depth to be negligible during the night.

Methods

Sampling and Processing

Lakes were chosen for sampling by comparing DOC concentrations from previous sampling. DOC values for Hummingbird Lake and Roach Lake were determined by taking water samples from a depth of 0.5m at the deepest point in the lake. Those samples were filtered through a Whatman 47mm GFF. The filtrate was then preserved in an acidic solution (pH ~3) of dilute H₂SO₄ and then analyzed for DOC. DOC samples for Long Lake were collected as the filtrate of epilimnetic water by passing through precombusted (4 h at 450°C) Whatman GF/F glass fiber filters under low vacuum pressure (less than 10 cm of Hg). The filtrate was collected directly in precombusted glass scintillation vials (4 h at 550°C) and then sealed and frozen until analysis. The DOC samples were analyzed on a Shimadzu model 5050 high temperature TOC (total organic carbon) analyzer at the University of Notre Dame in South Bend, IN and at the USDA Forest Service Northern Research Station in Grand Rapids, MN. Hummingbird Lake was assigned a "High DOC" category (24.38 mg/L), Long Lake was assigned a "Medium DOC" category (8.27 mg/L), and Roach Lake was assigned a "Low DOC" category (2.6 mg/L).

Random sampling locations in each lake were assigned within the deepest portions (> 5 meters) of each lake. Two sites on each lake were assigned for each sampling episode. A sampling episode was defined as sampling the same two sites during the afternoon and at night on the same day.

Day sampling always occurred between 1 and 3pm. Night sampling always occurred between 10:30pm and 12:00am. Once at a site during the day, dissolved oxygen (DO), % saturated oxygen, and temperature using a YSI Pro 20 or a YSI Professional Plus would be measured. Readings using the YSI Pro 20 and Professional Plus were collected first just below the surface of the water and then once every meter below that until reaching the bottom of the lake. Light intensity was measured with a LI-250A Light Meter. A measure of terrestrial light intensity was first measured by taking a reading with the sensor just above the surface of the water. Readings were then taken just below the surface of the water and every meter down until the bottom of the lake. *Chaoborus* spp. were sampled at each site using a Schindler-Patalis trap. Samples from the Schindler-Patalis trap were taken every meter starting at 1m and ending at the last depth that abiotic data were recorded. At night, *Chaoborus* spp. samples were collected at the same sites using the same method as the day. No abiotic data were collected at night. Schindler-Patalis trap samples were taken back to the lab where all *Chaoborus* spp. from each sample were counted.

Statistical Analyses

To account for differences in lake depth, raw counts of *Chaoborus* spp. larvae were not used. To determine what relative depth the majority of *Chaoborus* spp. larvae could be found at or above, *Chaoborus* spp. larvae at every meter for every site were counted, starting at 1m and going down from there, until a depth that would put the count over half of the total amount of

Chaoborus spp. larvae at that site was reached. That depth would then be divided by the total depth of the site to make it a relative depth. This conversion was used for both night and day samples. A one-way ANOVA with a Tukey post-hoc test was ran for the day and night samples (the night sampled were transformed) to determine whether the relative daytime distance of *Chaoborus* spp. larvae from the surface of the water was significantly different between DOC categories. Relative distance from the surface of the water during the day was fit to three separate linear regression models as a function of DOC, light intensity, and temperature and the transformed nighttime data were fit to a regression as a model of DOC.

To further understand the placement and displacement of *Chaoborus* spp. larvae sites were broken into three stratification layers: the epilimnion, the metalimnion, and the hypolimnion. What percentage of *Chaoborus* spp. larvae at each site were in each of the stratification layers was then determined. Daytime data were normalized using a square root transformation and percent distribution of *Chaoborus* spp. larvae for night and day were compared across lakes and stratification layers using a 2-way ANOVA.

To find out where the average sampled *Chaoborus* spp. larvae would be found in the study lakes, what depth the average *Chaoborus* spp. larvae was found in at each site and then divided by the maximum depth at the respective site to get a relative depth. Daytime and nighttime converted data used in two one-way ANOVA's with Tukey's post hoc tests for both sets of data with DOC category as the categorical variable in both cases and daytime relative depth and nighttime relative depth as the respective response variables. The same converted data was used to examine the difference between average *Chaoborus* spp. larvae depth at day and night in each of the different lakes. Paired t-tests were used on the data from Long Lake and

Roach Lake and a Wilcoxon Signed-Rank Test, the non-parametric equivalent of a paired t-test, was used on the data from Humminbird Lake since the data from daytime was not normal.

To determine whether the displacement of the average *Chaoborus* spp. larvae from daytime to nighttime differed between DOC categories, the average *Chaoborus* spp. larvae nighttime depth at each site was subtracted from the average *Chaoborus* spp. larvae daytime depth. A one-way ANOVA with a Tukey's post-hoc test with DOC category as the categorical variable and the average *Chaoborus* spp. larvae displacement as the response variable was ran. To determine whether the relative displacement of the average *Chaoborus* spp. larvae differed between lakes, the displacement from each site was divided by the maximum depth at the respective site. Once converted, the data were used to run a one-way ANOVA with DOC category as the categorical variable and relative displacement as the response variable.

All statistical tests and transformations were done in R. All data conversions were done in Excel.

Results

Relative Depth of the Majority of Chaoborus spp.

During the day there were significant differences in the relative depth of the majority of *Chaoborus* spp. larvae between the DOC categories ($F=9.728$, $df=2$, $p=0.001$). The relative depth of the majority of *Chaoborus* spp. larvae in the low DOC lake was significantly deeper than both the medium DOC lake ($p=0.02$) and the high DOC lake ($p<0.001$) (figure 4). There were significant relationships between the relative depth of the majority of *Chaoborus* spp. larvae during the day and DOC ($R^2=0.375$, $p=0.003$; figure 5), light intensity ($R^2=0.2807$, $p=0.01$; figure 6), and temperature ($R^2=0.205$, $p=0.04$; figure 7). There were also significant differences in the relative depth of the majority of *Chaoborus* spp. larvae at night ($F=36.37$,

df=2, $p < 0.001$). The relative depth in the low DOC lake at night was significantly deeper than both the medium DOC lake ($p < 0.001$) and the high DOC lake ($p < 0.001$) (figure 8). There was a significant relationship between the relative depth of the majority of *Chaoborus* spp. larvae and DOC ($R^2 = 0.569$, $p < 0.0001$; figure 9) at night.

Differences Between Stratification Layers

There were significant differences in the percent of *Chaoborus* spp. larvae in different stratification layers during the day ($F = 55.43$, $df = 2$, $p < 0.0001$; figure 10). There was also a significant interaction between the DOC category and the stratification layer ($F = 3.3172$, $df = 4$, $p = 0.02$; figure 11). At night there was no difference in the percent of *Chaoborus* spp. larvae in the different stratification layers ($F = 2.7$, $df = 2$, $p = 0.07$).

Night and Day Differences in Average Chaoborus Depth Within Lakes

There were significant differences between the depths of average *Chaoborus* spp. larvae at day and night in the low DOC lake ($t = 7.66$, $df = 7$, $p < 0.001$; figure 12), the medium DOC lake ($t = 4.88$, $df = 7$, $p = 0.002$; figure 12), and the high DOC lake ($V = 36$, $p = 0.008$; figure 12).

Relative Depth of Average Chaoborus

There were significant differences between the depth of the average *Chaoborus* spp. larvae between DOC categories during the day ($F = 33.61$, $df = 2$, $p < 0.0001$). There were significant differences between the low DOC lake and the high DOC lake ($p < 0.001$), the medium DOC lake and the high DOC lake ($p = 0.02$), and the medium DOC lake and the low DOC lake ($p < 0.001$) (figure 13). At night there were also significant differences between the depth of the average *Chaoborus* spp. larvae between DOC categories ($F = 1546.6$, $df = 2$, $p < 0.0001$). There were significant differences between the low DOC lake and the high DOC lake ($p < 0.0001$) and the medium DOC lake and the low DOC lake ($p < 0.0001$) (figure 13).

Displacement of Average Chaoborus

The distance traveled by the average *Chaoborus* spp. larvae from day to night was not the same in all DOC categories ($F=3.692$, $df=2$, $p=0.04$). The distance traveled was significantly further in the medium DOC lake than in the high DOC lake ($p=0.047$) (figure 14). There were not, however, any significant differences in the relative distance traveled from day to night by the average *Chaoborus* spp. larvae ($F=1.35$, $df=2$, $p=0.281$).

Discussion

The analyses support parts of my hypotheses, but not all of them. Chaoborids in the high DOC lake did tend to be associated more with shallower depths than the chaoborids in the low DOC lake in all of my analyses. The chaoborids in the medium DOC lake, however, were not always more closely associated with relatively shallower depths than the chaoborids in the low DOC lake. Analyses showed that chaoborids followed similar patterns to their daytime positioning at nighttime and were still associated with relatively shallower depths in the high DOC lake than the low DOC lake.

One of the most important effects that DOC has on lakes is that it lowers light intensity by absorbing light (Wissel et al. 2003). This refractory DOC can substantially influence pelagic communities (Christensen et al 1996), including two major implications to chaoborids. The first is that when DOC absorbs light, it can lead to the epilimnion (the top layer of a lake) being shallower and warmer (Wissel et al. 2003). Fish are primarily visual predators (Stratton and Kesler 2011), so when increased DOC absorbs light and shrinks what should be a prime fish foraging location in the water column, it makes it easier for chaoborids to avoid predation. Secondly, increased light absorbance from the increased DOC can make the hypolimnion larger, decreasing the area of the lake where there are livable amounts of dissolved oxygen for

fish(Wissel et al. 2003). With these facts in mind, the results I found make sense. Hummingbird Lake, the highest DOC lake, had a proportionally much larger hypolimnion than Roach Lake, the low DOC lake, and a slightly larger hypolimnion than Long Lake, the medium DOC lake (table 1).

My findings support past studies which suggest that chaoborids not only exhibit DVM, but also that migration could be influenced by DOC (Wissel et al. 2003). *Chaoborus* residing higher in the water column in high DOC lakes can have significant implications for the entire aquatic ecosystem. A previous study by von Ende at UNDERC (1979) suggests that fish predation is the major factor responsible for the absence of certain species of *Chaoborus*, so if that is true and there are fish present in the lake, then something must be stopping the fish from eating the chaoborids. Since chaoborids are closer to the surface in high DOC lakes, then this suggests that fish might not be able to see them very well, or else they would be eating them and lowering their presence in shallower waters.

A lack of predation on chaoborids could have large impacts on a lake's ecosystem as well. *Chaoborus* have been noted to have a substantial top-down effect on zooplankton (Liljendahl-Nurminen 2006). Therefore, if fish are not predating on the chaoborids, the chaoborids could significantly lower the abundance and/or diversity of zooplankton or take the place of fish as the major planktivore within the lake. Carpenter et al. observed that an increase in planktivores causes a decrease in zooplankton (1987). Another study by Wissel et al. showed that when *Chaoborus* were more abundant, zooplankton communities tend to shift from small zooplankton to large ones (2003). Since many fish in lakes are planktivorous and rely on the presence of zooplankton to eat and live, a decrease in zooplankton abundance caused by an increase in chaoborid abundance could adversely influence the abundance of planktivorous fish

and if planktivorous fish are adversely affected, then piscivorous fish could also end up decreasing in abundance or alter their diet to make up for a lack of fish to eat.

Potential change to an ecosystem is not the only impact that this cascade effect caused by an increase in DOC could create. If fish populations are negatively impacted by an increase in *Chaoborus* abundance in lakes with high DOC, then there could be an economic downside as well. Less fish in a high DOC lake could lead to less people fishing. Less people fishing would, in turn, mean less money spent on fishing supplies and gas to get to fishing lakes. In areas surrounding UNDERC, for instance, recreational fishing is a popular activity and less people fishing could hamper local economies. Hampered fishing is not the only way that increased DOC in lakes could influence human activity. When it comes to swimming, people tend to like to swim in clear bodies of water. High DOC lakes, however, have poor visibility and have an (by typical human standards) undesirable color.

It is hard to ignore the potential effects of increased DOC since it has been steadily increasing in aquatic ecosystems over the past several decades (Sucker and Krause 2009). What makes it an even more relevant topic to consider is that some increase in DOC can be traced to human activity. Soil disturbance, from plowing for instance, disrupts soil structure which can increase the likelihood of erosion, increasing the amount of organic matter that gets into freshwater systems (Stanley et al. 2011). With the influence of human activity on DOC and how an increase in DOC could influence natural ecosystems as well as ecosystem services in mind, more thought should be given to management and policy decisions concerning DOC levels.

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Tables

Table 1. Percent of Water Column Taken up by Each Stratification Layer. In the high and medium DOC lakes, the hypolimnion was much larger percent of the water column than in the low DOC lake.

Lake DOC Category	Stratification Layer	Average Percent of Water Column
High	Epilimnion	19.17
High	Metalimnion	36.25
High	Hypolimnion	44.58
Low	Epilimnion	68.55
Low	Metalimnion	15.72
Low	Hypolimnion	15.72
Medium	Epilimnion	23.69
Medium	Metalimnion	33.45
Medium	Hypolimnion	42.85

Figures

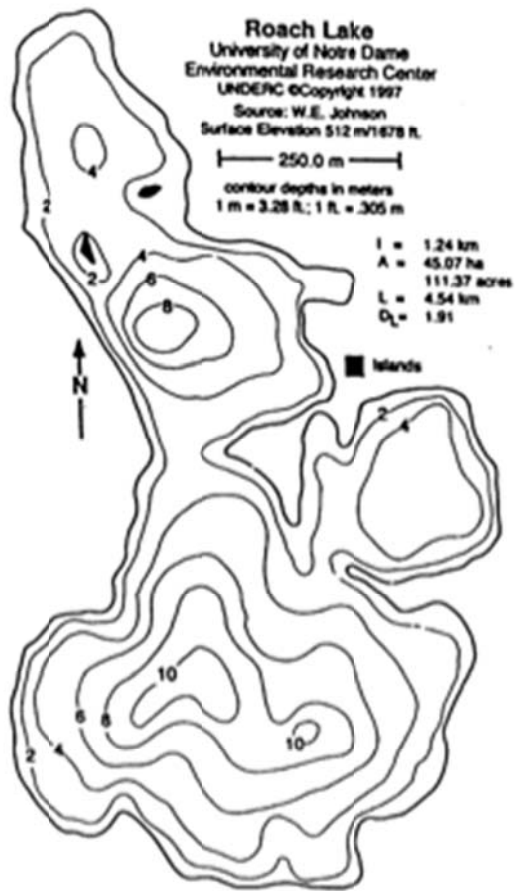


Figure 1: Roach Lake. This is a large seepage lake with a surface area of 45.07 hectares. Yellow perch, largemouth bass, pumpkinseed, and muskellunge are found in this lake (Aquatic Habitat Descriptions, UNDERC).

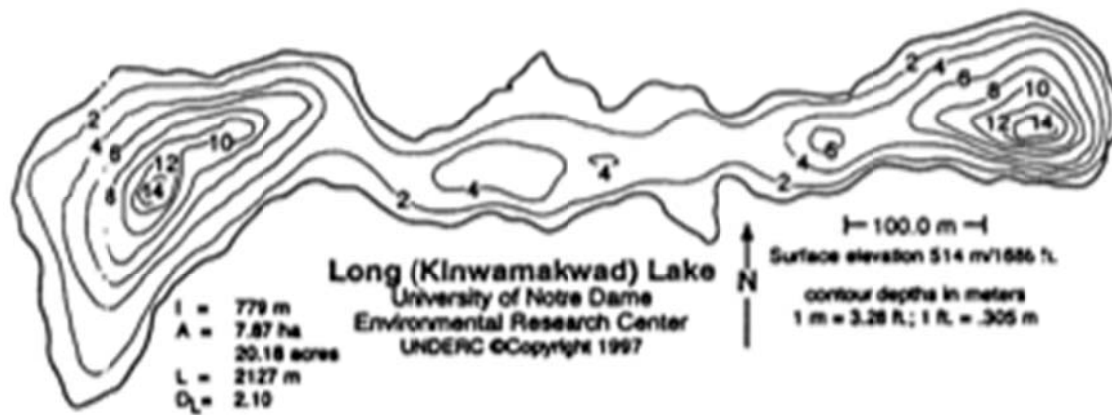


Figure 2: Long Lake. This is a fairly small (7.87 hectares), dumb-bell shaped lake. It contains a good population of both largemouth and smallmouth bass (Aquatic Habitat Descriptions, UNDERC).



Figure 3: Humminbird Lake. This is a tiny lake (0.76 hectares) with a population of yellow perch present (Aquatic Habitat Descriptions, UNDERC).

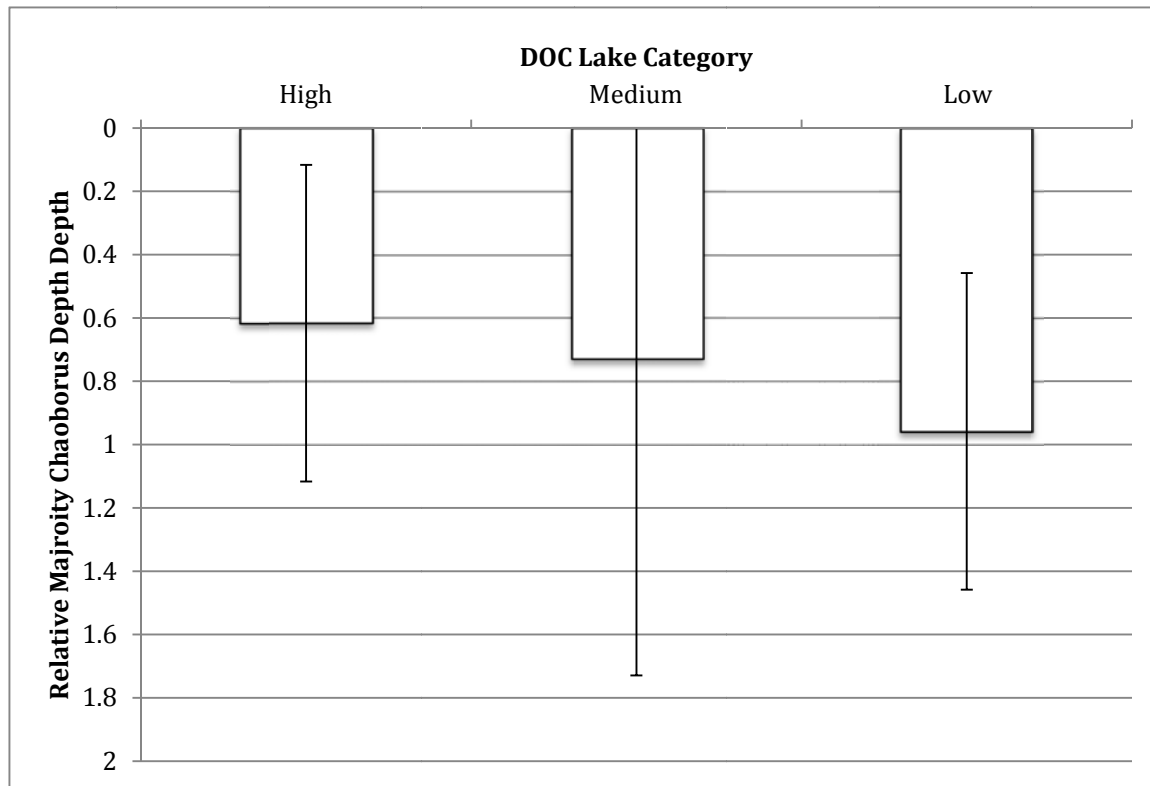


Figure 4: Relative Depth at which the Majority of *Chaoborus* are Found During the Day. The relative depth was significantly different between high and low DOC lakes (SE=0.07801 $p<0.001$) and medium and low DOC lakes (SE=0.07801, $p=0.02$).

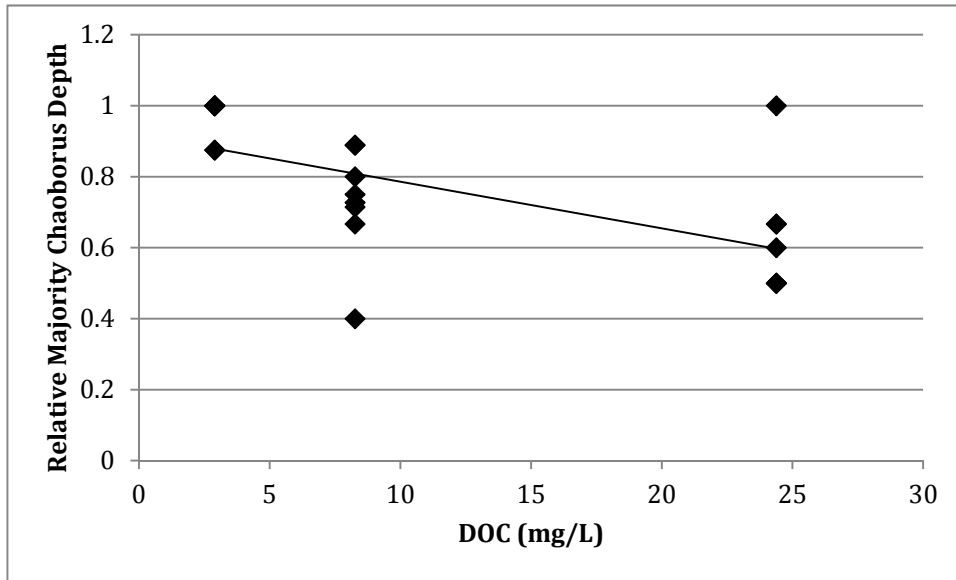


Figure 5: Regression between Relative Depth at Which Majority of *Chaoborus* are above and DOC During the Day. There was a significant negative relationship between the relative depth at which the majority of *Chaoborus* were at or above and the DOC (SE=0.1609, $R^2=0.3746$, $p=0.003$).

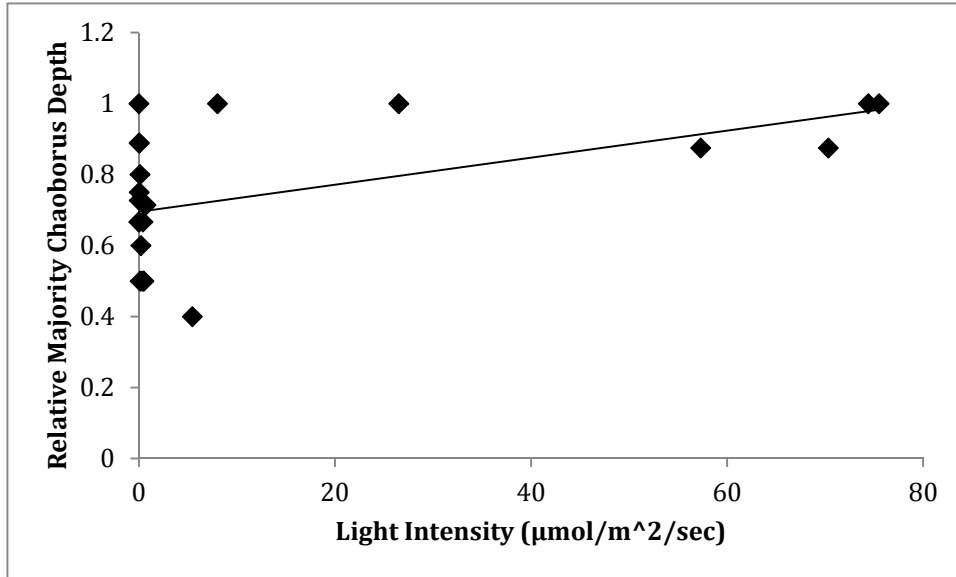


Figure 6: Regression Between the Relative Depth at Which Majority of *Chaoborus* are Above and Light Intensity During the Day. There was a significant positive relationship between the relative depth at which the majority of *Chaoborus* were at or above and the light intensity (SE=0.1725, $R^2=0.2807$, $p=0.01$).

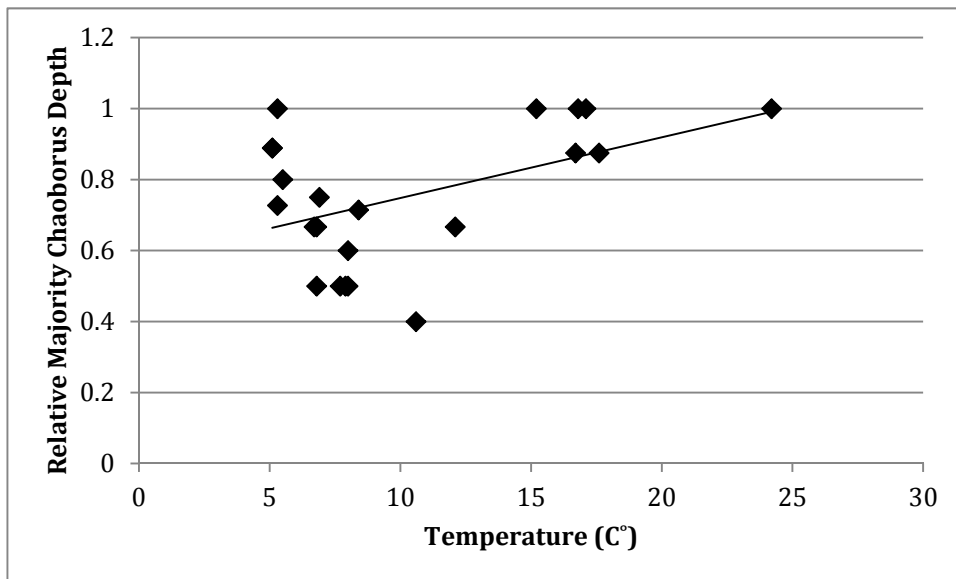


Figure 7: Regression of Relative Depth at Which Majority of *Chaoborus* are Found at or Above and Temperature During the Day. There was a significant positive relationship between the relative depth at which the majority of *Chaoborus* were at or above and temperature (SE=0.1813, $R^2=0.2054$, $p=0.04$).

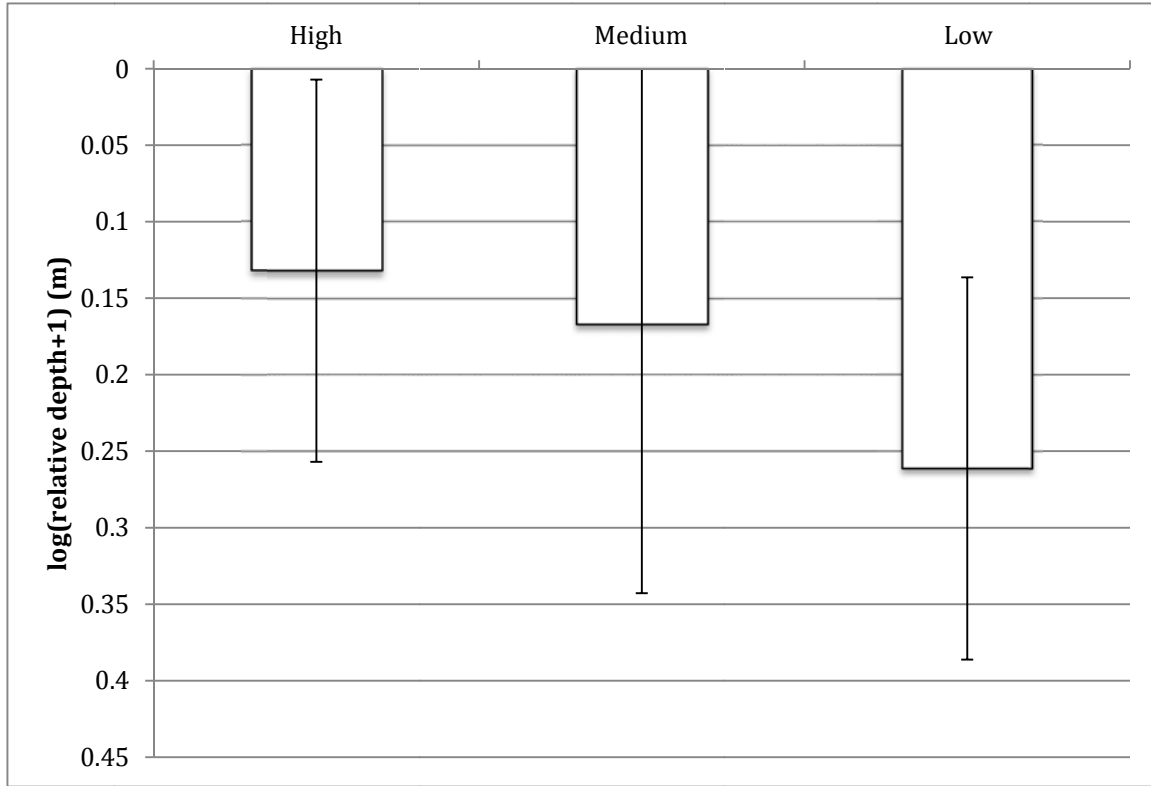


Figure 8: The Log of the Relative Depth at which the Majority of *Chaoborus* are Found at Night. There were significant differences between low and high DOC lakes ($SE=0.03612$, $p<0.001$) and between medium and low DOC lakes ($SE=0.03612$, $p<0.001$).

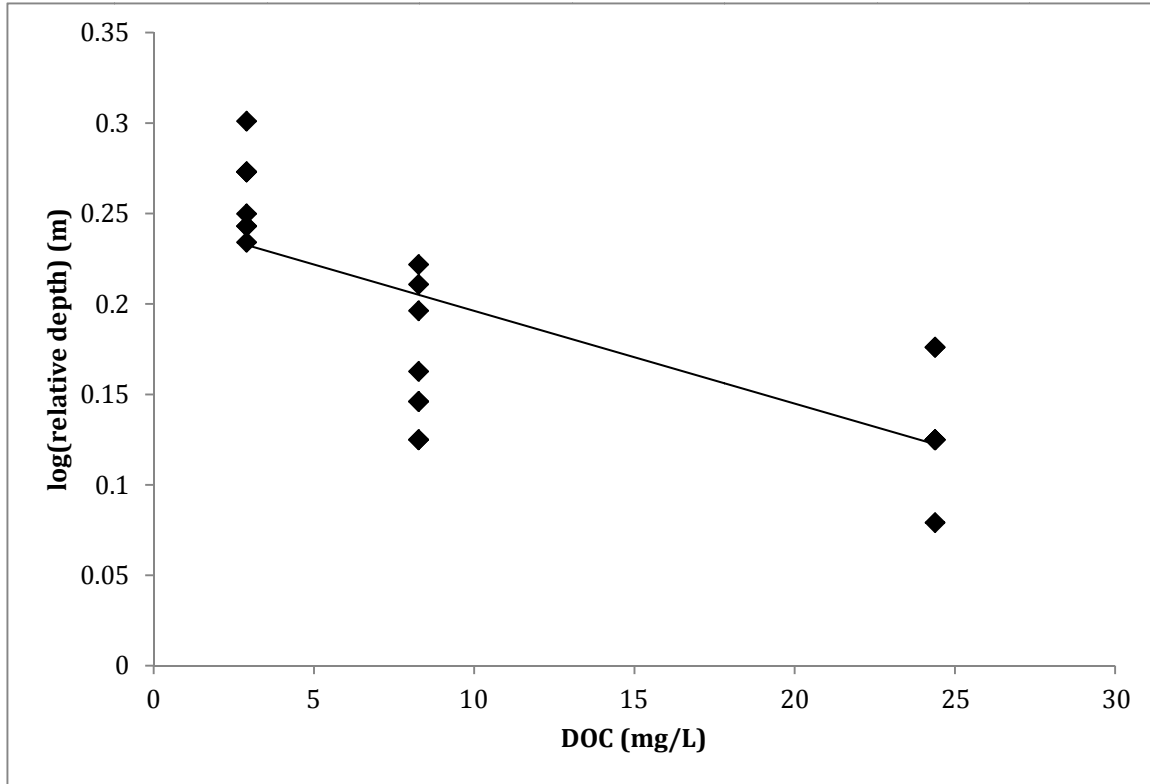


Figure 9: Regression between the Log of the Relative Depth at Which the Majority of *Chaoborus* are Located and DOC at Night. There was a significant negative relationship with DOC (SE=0.09786, $R^2=0.5693$, $p<0.0001$).

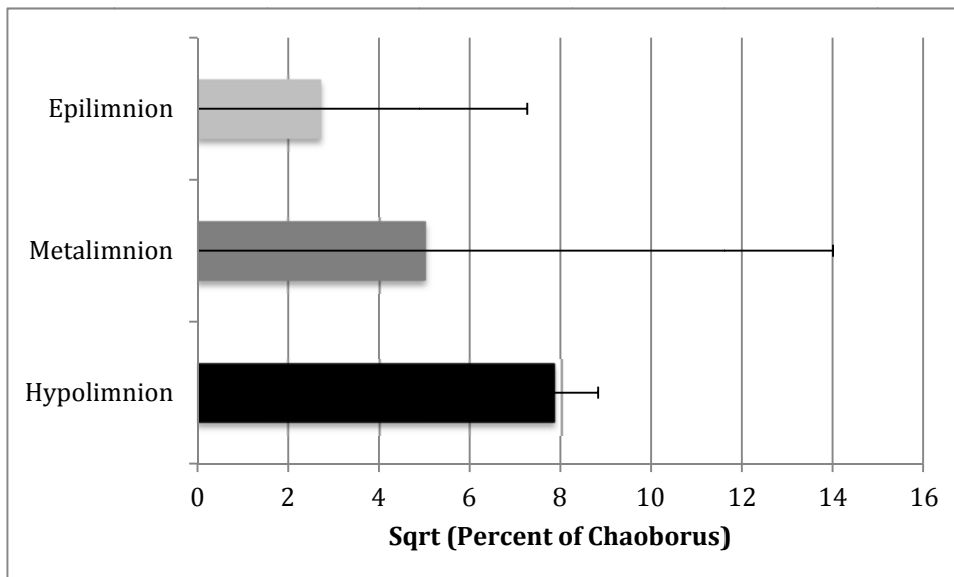


Figure 10: The Square Root of the Percentage of *Chaoborus* found in Each Stratification Layer During the Day. There were significant differences between the percent of *Chaoborus* found in the layers ($F=55.43$, $df= 2$, $p<0.0001$).

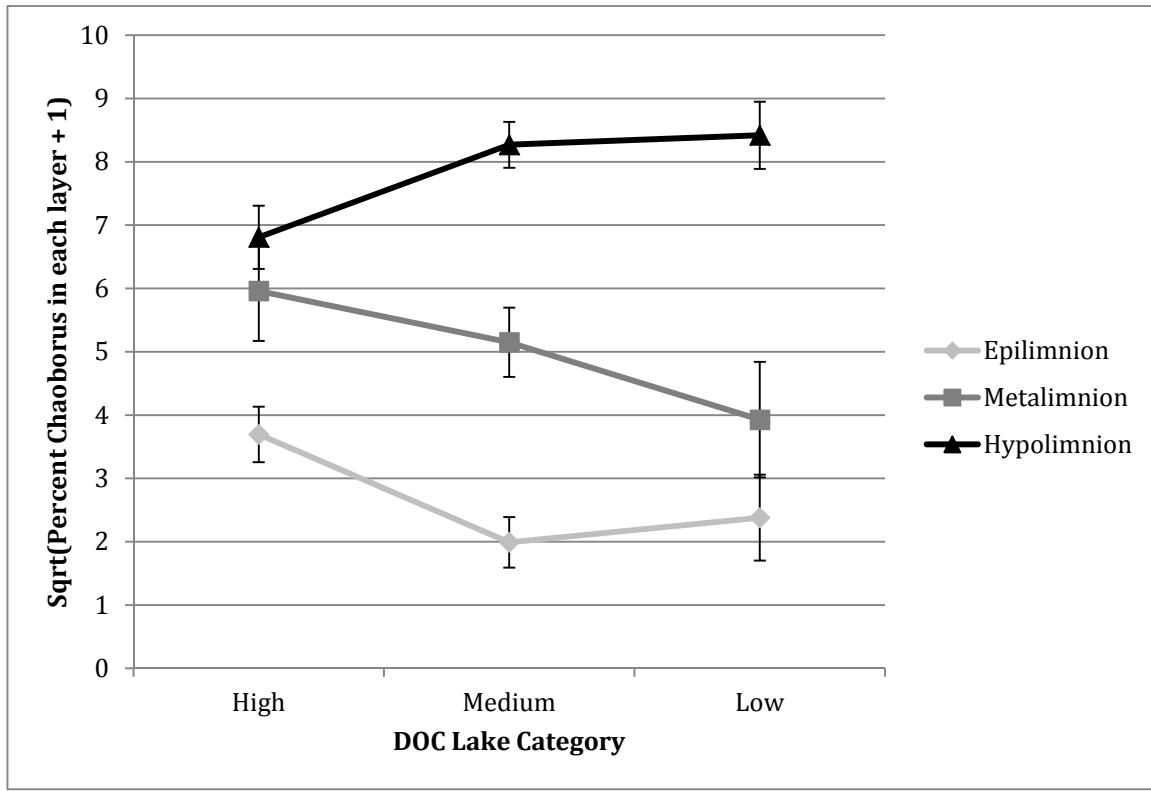


Figure 11: The Interaction Between DOC Category and Stratification Layer. There was a significant interaction term between DOC Category and Stratification layer ($F=3.3173$, $df=4$, $p=0.02$). The percent of chaoborids in the epilimnion and metalimnion increased over the DOC gradient and the percent of chaoborids in the hypolimnion decreased over the DOC gradient.

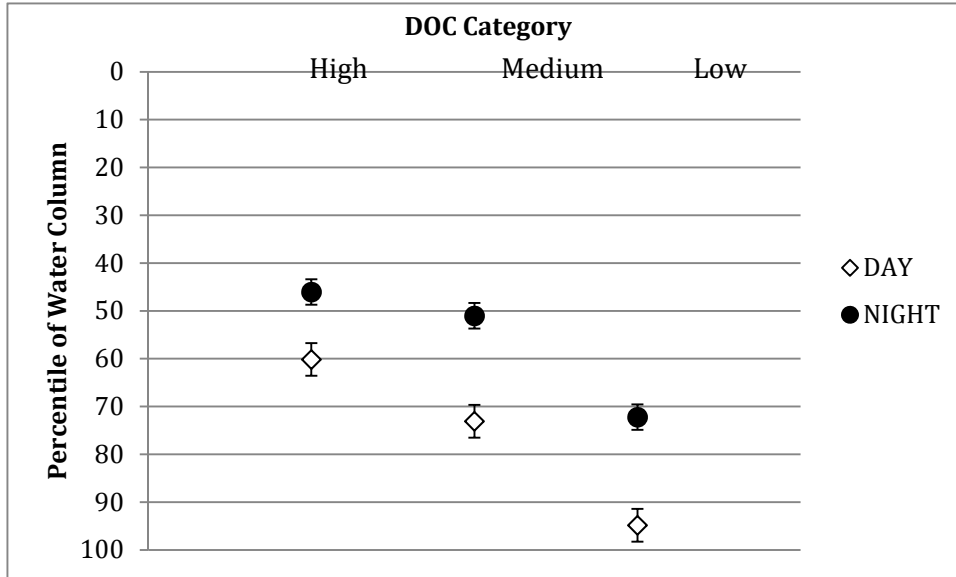


Figure 12: Relative Depth of Average *Chaoborus* at Night and Day in Different DOC Lakes. The relative depth of the average *Chaoborus* was significantly different between night and day in the high DOC lake ($V=36$, $p=0.008$), the medium DOC lake ($t=4.8834$, $df=6$, $p=0.002$), and the low DOC lake ($t=7.6565$, $df=7$, $p<0.001$).

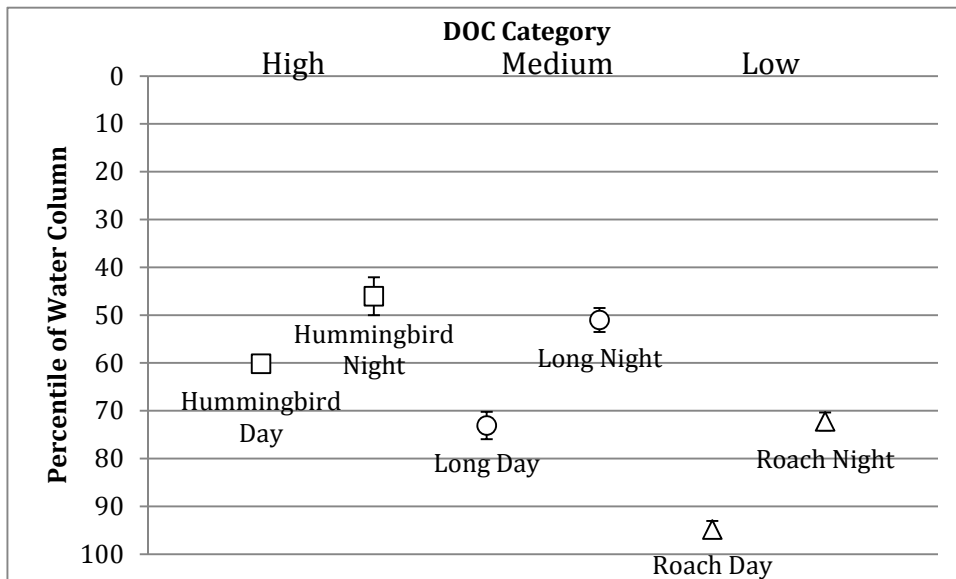


Figure 13: Relative Depth of *Chaoborus* at Night and Day in all DOC Categories. There were significant differences between high and medium DOC lakes ($p=0.02$), the high and low DOC lakes ($p<0.001$) and the medium and low DOC lakes ($p<0.001$) during the day. At night there were significant differences between the low and high DOC lakes ($p<0.0001$) and the medium and low DOC lakes ($p<0.0001$).

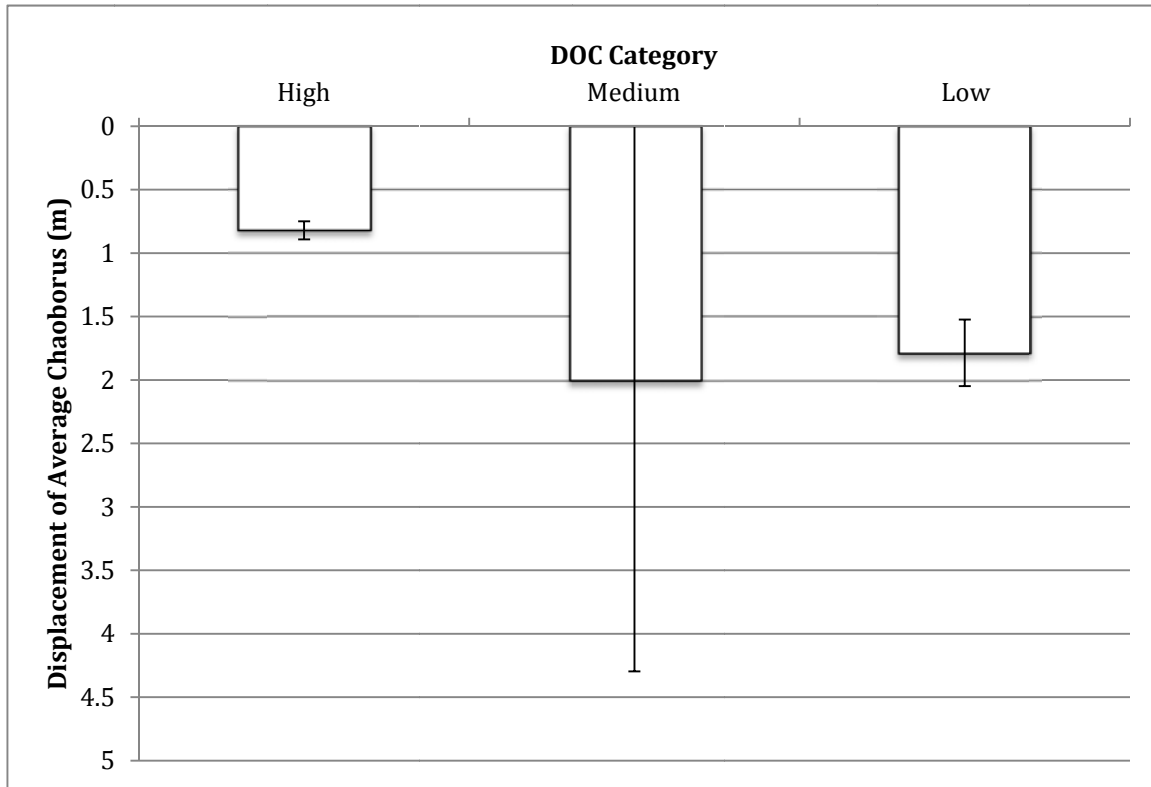


Figure 14: The Displacement of the Average *Chaoborus* in Different DOC Categories. The average chaoborid in the medium DOC lake traveled significantly further than the average chaoborid in the high DOC lake ($p=0.047$).