Diel vertical movement of zooplankton in Douglas Lake as a mechanism of predator avoidance and optimal foraging.

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ABSTRACT

Diel vertical movement (DVM) of zooplankton has been shown to follow a pattern of evening ascent and morning descent in response to light levels, amount of food, and risk from visually dependent predators. Since zebra mussels have colonized Douglas Lake, they have potentially altered the typical zooplankton migratory patterns by affecting phytoplankton abundance, productivity and water transparency. We hypothesized that zooplankton migration would be consistent with optimal foraging theory and influenced by fish predation. We predicted higher concentrations of zooplankton where there are higher concentrations of phytoplankton and a stronger correlation at night than during the day. Diel samples of zooplankton and chlorophyll were collected and further analyzed to determine the strength of their linear relationship. There was not a significant linear relationship observed between concentrations of zooplankton and chlorophyll during the day or at nighttime. DVM of zooplankton was observed in Douglas Lake prior to the colonization of zebra mussels, and our results suggest that zebra mussels may have altered the previously described DVM of zooplankton. A trend was observed in our results that, on average, there was a stronger relationship between zooplankton and chlorophyll during the night than during the day. This trend is statistically insignificant, but more sampling may increase the certainty of this relationship. Our results provide support for studies that describe how zebra mussels affect lake ecosystems and might indirectly affect zooplankton behavior.

INTRODUCTION

Diel vertical movement (DVM) in water columns is a well-documented biological phenomenon for both phytoplankton and animal species. The normal pattern is an evening ascent and a morning descent (Lampert 1989). This migration behavior is consistent with what is known about the optimal foraging theory, which suggests that zooplankton will maximize energy gains, while minimizing energy losses. They maximize energy gains by ascending to areas that have a higher concentration of phytoplankton at night. These migration patterns are related to light levels, presumably as a response to food (Clarke 1934). While Clarke's early work suggests light levels and amount of food seem to play an important role in migration patterns, there are other factors that may contribute to the complexity of zooplankton DVM.

Previous studies have proposed several hypotheses to explain DVM of zooplankton, suggesting predator avoidance (Zaret and Suffern 1976), advantages of increased genetic exchange (David 1961), more efficient phytoplankton and energy utilization (Hardy 1956), or increased fecundity (McLaren 1963). Only the influence of predator avoidance on zooplankton migration was focused on in our study. Zaret and Suffern (1976) showed that zooplankton vertical migration would result when populations are under intense, selective pressures from visually dependent predators. Further research suggests that migrants can safely exploit the resources of the upper strata at night and avoid predation during the day (Pijanowska and Dawidowicz 1987). Gliwicz (1986) examined nonmigratory and migratory populations of copepods and reported that diel vertical migrations are not apparent in lakes without predatory fish. This comparison between lakes with and without predatory fish suggests that fish predation plays a significant role in zooplankton migratory behavior.

Following the introduction of zebra mussels in many Michigan lakes, studies have shown that this invasive species can have spatial effects on phytoplankton productivity and influence abundance. Fahnenstiel et al. (1995) showed that presence of zebra mussels causes a spatial shift in primary productivity, with the potential to significantly alter other trophic levels and food webs. Further, because zebra mussels are filter feeders and in high density, they may have strong effects on the lake-wide phytoplankton biomass (Heath et al. 1995). Maguire and Grey (2006) found that zebra mussel colonization can cause dietary shifts in zooplankton but suggested this trend would be different in other lakes. Other research has shown that zebra mussels affect water transparency (Heath et al. 1995), which could potentially affect predation risk and subsequently zooplankton migration. Changes in phytoplankton productivity, abundance, and water transparency may alter migratory behavior of zooplankton.

In Douglas Lake, zebra mussels may have impacted trophic levels such that the migratory behavior of zooplankton has adjusted accordingly. In 1988, prior to zebra mussel colonization in Douglas Lake, Snoddy (1988) found that zooplankton were in greatest abundance at lower depths during the day than at night, consistent with optimal foraging theory. The effects of zebra mussels on zooplankton have not been fully characterized and seem to vary between lakes. Due to the presence of zebra mussels in Douglas Lake, a study of zooplankton migration would increase understanding of the effects that zebra mussels can have phytoplankton, zooplankton, and subsequently on lake food webs. A better understanding of the effects that zebra mussels have on lake food webs would have implications for the management of zebra mussels in Michigan lakes.

Hypotheses

We studied the distribution of phytoplankton and their predators, zooplankton, in Douglas Lake to see if zooplankton migratory behavior is consistent with what is known about optimal foraging theory. We hypothesized that migratory behavior of zooplankton is consistent with the optimal foraging theory and predicted a higher concentration of zooplankton where there is a higher concentration of phytoplankton, as measured by chlorophyll concentration. Further, we hypothesized that zooplankton migration is also influenced by predation by planktonivorous fish and predicted a stronger correlation between concentrations of zooplankton and chlorophyll at night than during the day.

METHODS

Field Sampling

Water samples were collected from the South Fishtail Bay of Douglas Lake in Pellston, Michigan during daylight (1:00PM - 3:00 PM) and after sunset (10:00 PM - 12:00 AM). All sample collection was done during May and June of 2007. Water samples of six liters were collected using a Van Dorn at each of eight depths: 1 m, 2 m, 4 m, 6 m, 8 m, 10 m, 12 m, and 14 m. Five liters from each depth were filtered through a type-10 (mesh size=153 microns) zooplankton net and the zooplankton was concentrated into approximately 10-15 mL of water. One liter from each depth was stored in a chilled, dark cooler for future measurement of chlorophyll.

Zooplankton Analysis

Live zooplankton were counted within two hours of collection. A dissection microscope and plates with eight 0.25 mL wells were used to count the zooplankton. The absolute number of zooplankton was approximated by counting a 10 mL sub-sample. Zooplankton were categorized by class as either maxillopoda (subclass: copepoda) or branchiopoda. Due to low numbers of branchiopoda, only maxillopoda were analyzed further. Zooplankton concentration was determined for each depth by counting the number of zooplankton and dividing the number by the five liters of water that was filtered through the Van Dorn.

Chlorophyll Analysis

Immediately following water collection, chlorophyll was sampled by filtering 120 mL of water using type HA 0.45-μm filters. Filters were stored in a freezer until analysis. The chlorophyll filters were placed in a 90% acetone solution buffered with magnesium carbonate, sonicated to break up algal cells, and extracted for 24 hours at -20° C (Wetzel 2000). Chlorophyll concentration was then determined using a Turner (TD-700) fluorometer according to the chlorophyll analysis method in Wetzel (2000).

Statistical Analysis

The strength of the linear relationship between concentrations of zooplankton and phytoplankton was determined by regression analysis (SPSS v. 15.0). Six regression tests were used to analyze the strength of the zooplankton and phytoplankton relationship between night and day for three separate dates. An alpha value of 0.05 was used for all tests.

RESULTS

For each sampling during the day and night, the linear relationships between the concentrations of zooplankton and chlorophyll were not significant (Figures 1A and 1B). During the day, the slopes were 0.038 (May 30, R^2= 0.013, p-value = 0.785), 1.234 (June 02, R^2 = 0.381, p-value = 0.103), and 0.156 (June 03, R^2 = 0.200, p-value = 0.267). During the night, the slopes were, 0.283 (May 30, R^2 = 0.467, p-value = 0.062), 0.564 (June 03, R^2 = 0.076, p-value = 0.510), and 0.497 (June 06, R^2 = 0.106, p-value = 0.432). Although the relationships were not significant, the trend of slopes for the nighttime samples was larger than for the daytime samples.

DISCUSSION

Our results failed to reject the null hypothesis that there would be no correlation between the distribution of phytoplankton and that of zooplankton. The results also failed to reject the null hypothesis that there would be no difference in the strength of the correlation between daylight and nighttime sampling.

We also failed to observe the well-documented DVM of zooplankton. No pattern was seen to follow the familiar evening ascent and a morning descent (Lampert 1989). While Clarke

(1934) explains that the DVM pattern will be a result of light levels, and subsequently chlorophyll levels, we could see no similar relationship with chlorophyll sampling and the abundance of zooplankton. In failing to find a significant relationship between zooplankton and phytoplankton, zooplankton migration in Douglas Lake is inconsistent with the optimal foraging theory. This lack of support for well-established patterns of zooplankton migration suggests that zebra mussels may have caused a deviation from what has been previously described in Michigan lakes.

The 1988 study by Snoddy showed the DVM of zooplankton in Douglas Lake, finding zooplankton in highest abundance at lower depths during the day than at night. Our results differed from the Snoddy study, finding no significant relationship between zooplankton and chlorophyll concentrations. The difference between our findings and the Snoddy study could be attributed to the zebra mussel colonization of Douglas Lake between 1988 and the time of our study. It has been shown that zebra mussels can have spatial effects on phytoplankton primary productivity and influence abundance (Fahnenstiel et al. 1995), with the potential to significantly alter trophic levels and food webs. Also, when zebra mussels are present and in high density, they may have strong effects on the lake-wide phytoplankton biomass (Mitchell 1996). Other research has shown that zebra mussels affect water transparency (Heath et al. 1995), which could potentially affect predation risk and subsequently zooplankton migration. Maguire and Grey (2006) found that zebra mussel colonization can cause dietary shifts in zooplankton. Our results provide support for these findings about how zebra mussels affect lake ecosystems and might indirectly affect zooplankton behavior.

While we cannot say conclusively that zebra mussels are affecting the migration of zooplankton in Douglas Lake, our results support the idea that introduction of zebra mussels may affect zooplankton behavior. Future studies of zooplankton migration in Douglas Lake should control for the zebra mussels to better characterize their effects. In light of our results, more sampling of chlorophyll and zooplankton concentrations would be helpful to increase the certainty of the relationship between zooplankton and chlorophyll. Figures 1A and 1B show a positive linear relationship, however this relationship is not significant (p-value > 0.05). During the night on May 30, the relationship between zooplankton and chlorophyll approached a significant finding (p-value = 0.062), but the correlation remained insignificant. This suggests that there may in fact be a significant relationship between zooplankton and chlorophyll that our data did not represent.

Conclusion

Our hypotheses were rejected because we did not find a significant correlation between zooplankton and chlorophyll concentrations. This may be due to a small sample size or the effect zebra mussel colonization has had phytoplankton productivity, abundance, water transparency, zooplankton diet, and potentially zooplankton DVM. This study further illustrates the wide-spread effects zebra mussels can have on lake ecosystems and supports the need for management of this invasive species.

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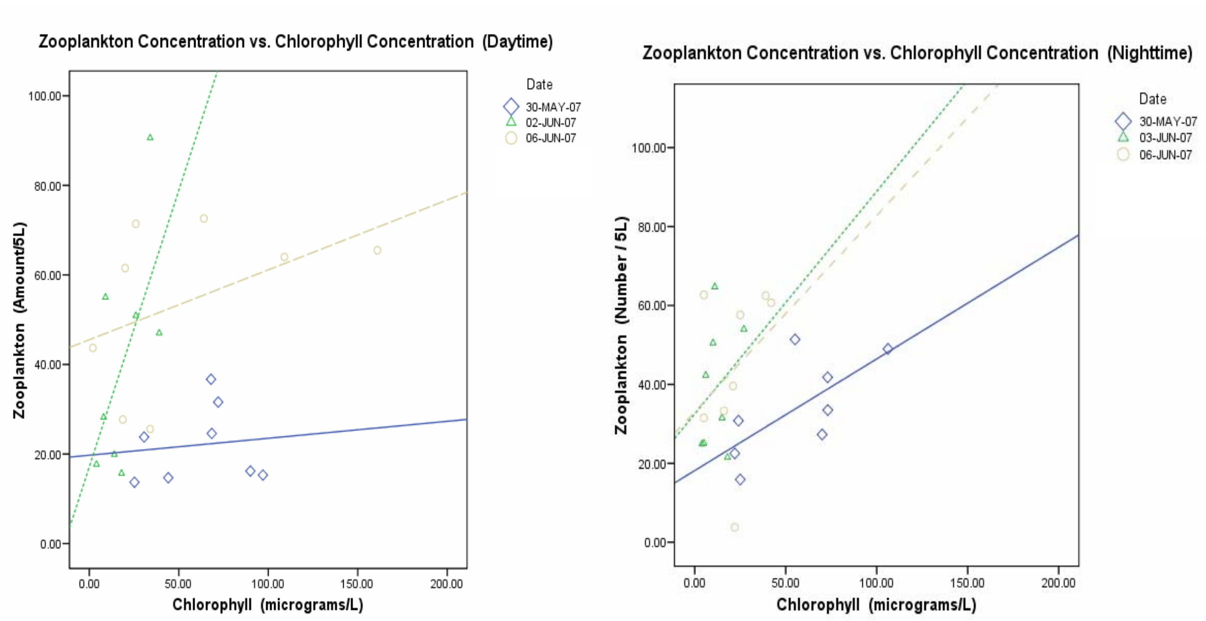

30-MAY-07
P value = 0.785
Slope = 0.038
R^2 = 0.013

02-JUN-07
P value = 0.103
Slope = 1.234
R^2 = 0.617

06-JUN-07
P value = 0.267
Slope = 0.156
R^2 = 0.447

30-MAY-07
P value = 0.062
Slope = 0.283
R^2 = 0.683

03-JUN-07
P value = 0.510
Slope = 0.564
R^2 = 0.275

06-JUN-07
P value = 0.432
Slope = 0.497
R^2 = 0.325

Figure 1(a) shows the linear relationship between zooplankton abundance and chlorophyll level during the day for the three sampling days. May 30 and June 6 have best fit lines that show little change of zooplankton abundance over a change in chlorophyll. June 2's best fit line shows that zooplankton increases rapidly with a slight increase in chlorophyll. However, these fit lines have been proved not significant. **(b)** shows the linear relationship between zooplankton abundance and chlorophyll abundance with an increase in chlorophyll. However, these fit lines also have been found not significant.