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Diel vertical migration strategies of zooplankton in oligotrophic Russell Pond, New Hampshire

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Abstract

Russell Pond is an ultra-oligotrophic lake with low chlorophyll a ($1.9 \mu\text{g L}^{-1}$), total phosphorus ($3.4 \mu\text{g L}^{-1}$), high Secchi Disk (10.4 m) and high light transmission (water coefficient of water, $k_w=0.33$). Vertical migration of *Chaoborus*, *Bosmina*, *Daphnia*, and copepods were examined using net collections of zooplankton discrete depth counts and sonar. Three contrasting patterns of vertical migration were observed in Russell Pond. *Chaoborus punctipennis* larvae vertical migration began at 7 pm and migrated through the entire lake water column, a total of 23 m from the sediments to the surface water in less than 4 hours, *Bosmina* had an epilimnetic migration, moving 3 m upward toward the surface between 4 and 6 pm but did not migrate further at 8 pm. *Daphnia* migrated downward (reverse migration) nearly 4 m, and the copepods did not migrate vertically. In contrast to the other macrozooplankton, the calanoid copepods stayed in the deep epilimnion, with no detectable vertical displacement. The variation in vertical migration patterns in Russell Pond illustrate how this adaptive diel behavior is tailored to the differing selective pressures on the different zooplankton species.

UNH Center Freshwat. Biol. Res.(2013)

Introduction

Diel vertical migration (DVM) is seen in both marine and freshwater zooplankton and can vary in amplitude based on taxa or species (Haney 1988). Often in the evening the zooplankton will ascend to the surface (nocturnal migration), while in the morning they will descend back into the deep waters. Varying of amplitude between zooplankton species could be influenced by turbidity and food abundance causing the organisms to either migrate up and down in narrow strips or be stratified in deep waters for the day before spreading out through

the water column at night. Nocturnal migration is utilized by zooplankton as an adaptive strategy to avoid visually feeding predators such as fish and avoid harmful UV radiation (Lampert 1989).

In reverse DVM the zooplankton population is found closer to the surface during the day, but migrates deeper at night. Reverse DVM may be explained by high levels of invertebrate predators that use tactile stimuli to locate their prey. DVM is more often coupled with the abundance of planktivorous fish (Hays 2003).

Chaoborus or phantom midge, are fly larvae that occur in most of our deep lakes. *Chaoborus* are tactile hunters who can sense vibrations up to 5 mm; and primarily eat microcrustaceans and rotifers when present in upper waters at night. The pigmented gas bladders that the larvae contain aid in their migration, as the sacs enlarge giving them a lower density than the water allowing the *Chaoborus* to move toward the surface. When the gas bladder muscles contract, the gas volume decreases and the larvae move downward (Cole 1994). *Chaoborus* larvae have a high risk of fish predation, which is thought to be one of the adaptations of their DVM (Berendonk 1999).

Acknowledgments

Thank you to Dr. James Haney, Dr. Alan Baker, and Jonathan Dufresne for their help on everything from data collection to data analysis. Data were collected during a lake study on Russell Pond in the Field Limnology class of 2013 at UNH. Therefore, I would like to thank all of the members of the class for aiding in the data collection, any help in the lab they may have provided, and for the general comradery that made the experience worthwhile. My lab partner, Deena Hardy, also deserves a huge thank you for spending numerous hours processing data and counting plankton samples with me. Lastly I would like to thank New Hampshire Lakes Lay Monitoring Program for the phosphorus and chlorophyll analysis, and Amanda Murby for the toxins analysis.

When *Daphnia* are exposed to visual predators, their migratory strength may depend on body size, as smaller individuals may remain in shallower water during the day compared to the larger animals (Beklioglu et al. 2008). The larger organisms are more conspicuous and therefore have to perform a stronger DVM when exposed to fish cues (Beklioglu et al. 2008).

We set out to observe migration patterns in Russell Pond using sonar and discrete depth plankton sampling. The focus of this study was to examine the migration patterns of the net zooplankton and the phantom midge larvae, *Chaoborus*.

Methods

Study Site

Russell Pond, visited on September 26, 2013, is an oligotrophic lake characterized by its high transparency and low nutrients and phytoplankton (Bailey and Davignon 1999). The mean depth of Russell Pond is 10.1 m and the maximum depth is 23 m (NH Fish and Game). Russell Pond is located in the White Mountain National Forest in Woodstock, NH at 4.00874409 latitude, -71.64892835 longitude (USDA). Adjacent to Russell Pond is campground complete with 86 wooded sites compacted with gravel and paved roadways (Campground Concessionaires 2010). The forest surrounding Russell Pond is mixed. The northern half is predominately deciduous trees, while the southern half is predominately conifers (Bailey and Davignon 1999). The most common zooplankton of Russell Pond are calanoid copepods *Daphnia pulex*, *Chaoborus punctipennis*, and *Bosmina longirostris*. The lake was visited for data collection on September 26, 2013.

Water Quality Sampling

A Yellow Springs Instruments Inc. 6600 M V2 Multi-Parameter probe that was equipped with a 650 MDS Data Logger was used to measure temperature (C), depth (m), dissolved oxygen (% & mg L⁻¹), chlorophyll a fluorescence (µg L⁻¹), phycocyanin fluorescence (equivalent to *Microcystis aeruginosa* UTEX # 2385 cells ml⁻¹), Redox (corrected to pH at E₇ at 20° C), specific

conductance (µS cm⁻²), turbidity (NTU), and pH. The depth sensor was calibrated to air for zero air pressure at the water surface. Before taking measurements, the multiparameter sonde was placed in the water for 5 min to further calibrate, and then lowered at a constant rate of 0.5 m min⁻¹ until the probe hit the bottom of the lake. The data were uploaded into YSI Ecowatch, exported into Excel and manipulated in Sigma Plot 12.5 with the Statistical package, SigmaStat.

Light and Transparency Measurements

A light probe equipped with a Li-Cor underwater and sky quantum sensors, and Radiometer 1400 data logger was used to measure light extinction. The data were uploaded and manipulated using Excel and Sigma Plot. The underwater sensor was lowered in 0.5 m increments, while the sky sensor remained on deck of the boat to measure incident light accounting for cloud movement and shade. The sensors were sensitive to photosynthetically active radiation (400-700 nm), and measured photosynthetic photon flow density (µmol photons m⁻²s⁻¹). A black and white secchi disk (20 cm diam) was used with a view scope to measure water clarity.

Sediment Core

A sediment core (6.4 cm diam) was obtained at 20 m depth using a benthic gravity corer (Aquatic Research Instruments, Inc) with 2 brass weights (9.1 kg). Two cm slices of sediment were collected in sample containers. Sediment samples were analyzed for organic matter by comparing the weight of dried samples (overnight at 60 C) with samples burned in a muffle furnace for one hour at 550 C to remove organic matter. The first two centimeters were used for toxin analysis.

Sonar

Sonar (Lowrance LCx 25-27C, frequency 200 khz) was used to track the vertical migration of *Chaoborus*. Electronic recordings of sonar transects were viewed Sonarview (Lowrance). Canoe transects were made with an even speed across the lake nearly every half hour during the hours of 3:30 to 7:30 pm (Fig 0).

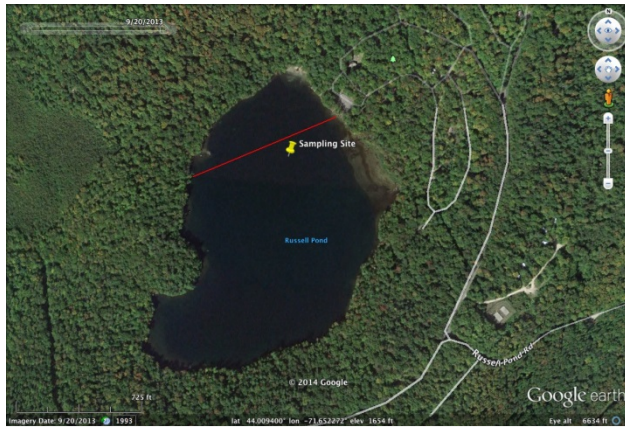


Fig 0: Russell Pond, NH. Red line depicts sonar transect (290 m), and yellow pin indicates the sampling location (Lat 44.010441, Long-71.652964, elevation 504 m (1654 ft). Image (1993) from Google Earth.

Plankton Sampling

Discrete plankton sampling was done with a 10 L Schindler-Patalas trap with a 50 μm cod end. The Schindler-Patalas was lowered from 0-14 m at approximately 3 pm. A closing net with mesh of 80 μm , an 80 μm cod end, 30 cm diameter, and 10 L volume was used to obtain depth profiles of plankton sampled at 2 m intervals from 0-14 m. Closing net samples were taken at 3 pm, 4 pm, 6 pm (pre-sunset), and 8 pm (post sunset) to evaluate vertical migration of zooplankton and *Chaoborus* larvae. Sampling each vertical series started roughly on the hour and lasted about 15 min. All times of day are daylight savings time in the Eastern time zone. Samples were preserved with formalin sucrose (Haney and Hall 1973).

To separate the zooplankton and phytoplankton three replicate plankton tows were taken from 12 m to the surface using a net with 80 μm mesh and a diameter of 20 cm. Each sample was placed into a light gradient bottle which was then filled to the top with water. After 20 min the first 250 mL was collected and filtered for zooplankton with a 50 μm mesh, and the rest of the sample was collected and filtered for phytoplankton.

Plankton were counted and identified to species (zooplankton) or family class (phytoplankton). Zooplankton obtained from the Schindler-Patalas were enumerated from the entire sample, while zooplankton obtained from closing nets were sub sampled. Phytoplankton was analyzed for relative percent abundance by

counting a total of 100 phytoplankters under 400X magnification. Zooplankton quartile distributions were calculated using the method described by Pennak (1943).

Integrated Tube Samples

Integrated tube samples were taken from 0-3 m using a Tygone tube with a 2.54 cm diameter. The samples were then used for analysis of chlorophyll a, microcystin, mercury, and total phosphorus.

Samples for chlorophyll extractions were filtered on 0.45 μm Millipore membrane filters (HAWP, 47 mm diam) filtered at psi<5. Filters were dried, stored in darkness on ice and later extracted in 90% Acetone (with MgCl) for 18-24 h and stored at 20 °C. Tissue grinding and 15 mL of Acetone broke down the filters which were then placed into a centrifuge for 20 min at 2000 rpm. Supernatants were poured into a cuvette and read in a spectrophotometer at 620, 630, 640, and 700 nm. The chlorophyll- α acetone extraction and the absorbic acid method used to analyze total phosphorus were performed using the standard operating procedures of the University of New Hampshire's Lakes Lay Monitoring Program (UNH LLMP 2010).

Results

Water Quality

A secchi disk depth of 10.4 ± 0.19 m, chlorophyll a concentration of 1.9 ± 0.68 $\mu\text{g L}^{-1}$, and total phosphorus concentration of 3.4 ± 0.23 $\mu\text{g L}^{-1}$ confirmed the oligotrophic status of Russell Pond (US EPA 2007). Trophic State Index (Carlson 1977) values were Secchi disk of 26.89 m, chlorophyll a of 36.90, and total phosphorus of 21.80; all of which classify Russell Pond as oligotrophic. The coefficient of light attenuation by water, k_w was 0.33 ± 0.01 . Detectable light penetrated to approximately 9 m (Figure 1). Cyanobacteria appeared to be concentrated in the epilimnion with maximum phycocyanin from 3-5 m (approx. 135 RFU or relative fluorescence units) (Figure 2). Chlorophyll a had a small maximum in deeper water at 11 m corresponding with a peak in

dissolved oxygen and pH (Figure 3), suggesting this deep chlorophyll a layer was photosynthetically active.

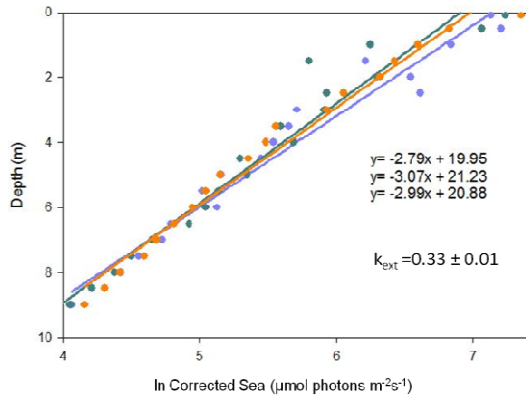


Fig. 1: Log-log relationship of depth (m) and underwater light ($\mu\text{mol photons m}^{-2}\text{s}^{-1}$). Lines represent linear regressions of three independent light series.

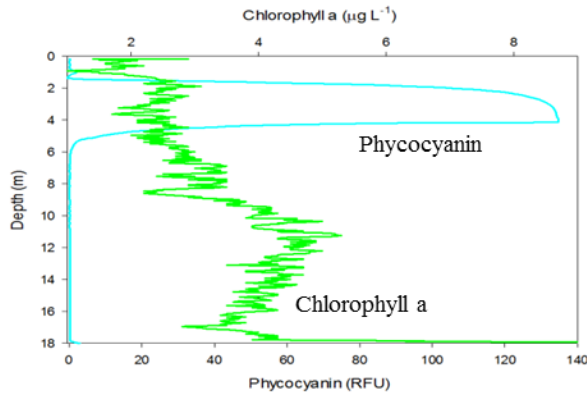


Fig. 2: Chlorophyll a and phycocyanin relating to depth.

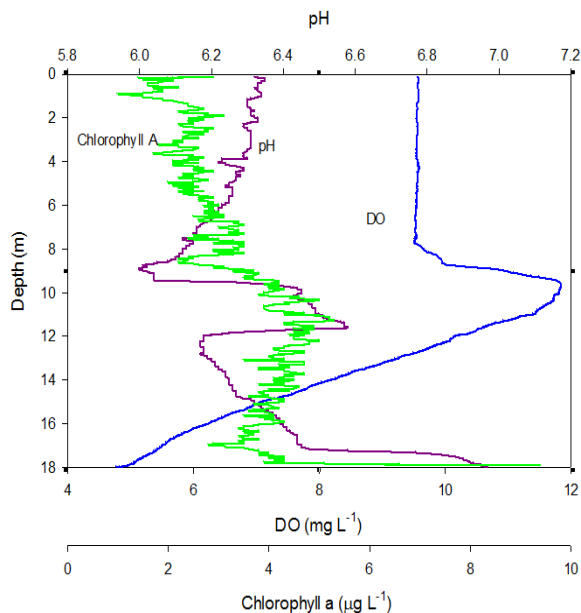


Fig. 3: Chlorophyll a, dissolved oxygen, and pH relating to depth.

Vertical Migration

Sunset on the date of sampling was 6:46 pm, so that only the sampling beginning at 8 pm was post-sunset. *Chaoborus* had a nocturnal DVM pattern, as there were none present at 3 pm or 4 pm, while at 6 pm they were found below 10 m, and at 8 pm, visual darkness, roughly 75 min after sunset, the majority of the planktonic population was above 4 m (Figure 4). Based on closing net samples of *Chaoborus* in the water column at the 8 pm sampling were roughly 10 times those measured at 6 pm (0.15 versus 1.7 larvae per liter), indicating a major recruitment of larvae from the sediments in this 2 h time interval. *Daphnia* underwent reverse DVM as they migrated downward almost 4 m after sunset (Figure 6), and were most numerous at depths 4-6 m during the day; and depths 8-10 m at night (Figure 5). Notably no *Daphnia* were detected from 0-2 m at 3 pm due to their larger size and the increased visibility in the top 2 m. Calanoid copepods had the highest densities, but did not show any pattern of vertical migration. *Bosmina* exhibited a pronounced ascent toward the surface of the lake, as at 3 pm the greatest abundance was at 5 m, while at 8 pm they were most numerous at 1 m (Figure 7). Most of the *Bosmina* were above the thermocline at approximately at 9 m (Figure 7).

Sonar graphs were utilized to compare *Chaoborus* to *Daphnia pulex*, Copepods, and *Bosmina* vertical positions from 3 pm to 8 pm (Figure 7). Whereas sonar signals of fish are strong and general appear as hatchet traces, sonar returns from tiny air sacs of *Chaoborus* larvae are much smaller and appear as small dots on the sonar graphs which can be seen rising throughout the time span of 3-8 pm but most collectively moving s from 7-8 pm. *Bosmina* migrate between 4 and 6 pm as their population distribution changes from 75% of the population being above 9 m at 3 and 4 pm to 75% of the population being above 6 m between 6-8 pm.

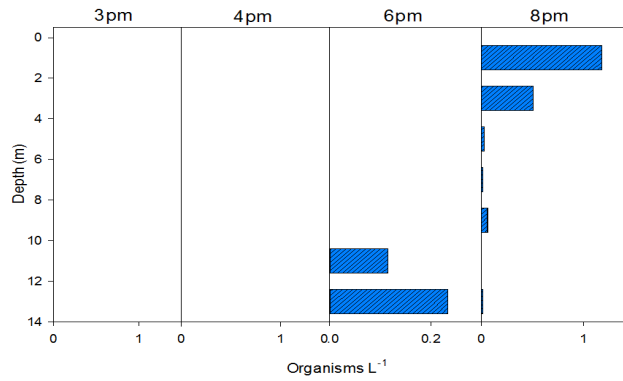


Fig. 4: Vertical distributions of *Chaoborus* larvae at 3 pm, 4 pm, 6 pm, and 8 pm estimated from closing net samples.

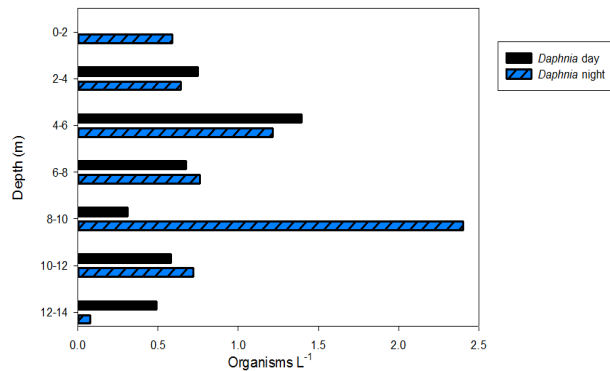


Fig. 5: *Daphnia* migration comparing day (3 pm) and night: post sunset (8 pm) densities from closing net samples.

The calanoid copepods as a whole do not show a distinct migration as 75% of the population remains above 10-11 m throughout 3-8 pm; but there does appear to be two separate populations one occurring from 1-5 m and another from 9-13 m. The 50% of the *Daphnia* population migrated downward as they were most concentrated from 4-6 m at 3 pm (1.5 organisms L^{-1}), while at 8 pm most concentrated from 8-10 pm (2.5 organisms L^{-1}) (Figure 6).

Discussion

The oligotrophic status of the lake may have an effect on the zooplankton, as it has been shown that in more oligotrophic conditions food availability may be poor to the point where an energy balance cannot be maintained, therefore causing the zooplankton to migrate (Lampert 1989). There is also a light-related mortality

hypothesis where zooplankton have been observed avoiding the epilimnion during the day as the light makes them more easily seen by predators (Lampert 1989). This may explain the *Chaoborus* migration as there were none present within the epilimnion until 8 pm, suggesting they may have been avoiding well lit parts of the lake so as not to be seen by predators.

Another factor of predation that may be affecting the migration of zooplankton is kairomones (Berendonk 1999). *Daphnia* have been known to develop neck spines in the presence of *Chaoborus* kairomones as well as

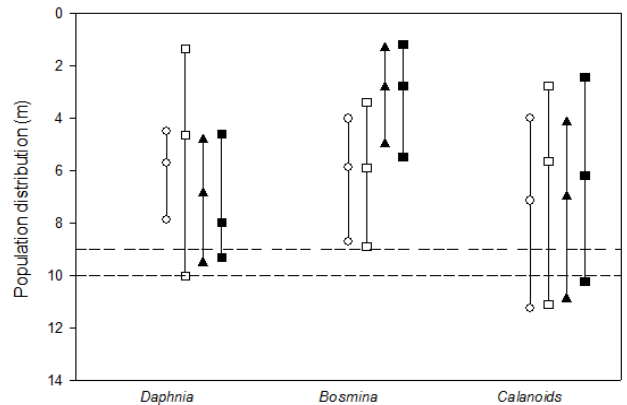


Fig. 6: Quartile graph: white circles = 3 pm, white squares = 4 pm, dark triangles = 6 pm, and dark squares = 8 pm. The dashed lines represent the thermocline boundaries. For each profile, the uppermost symbol depicts the depth above which 25% of the population is located, the second symbol, 50% of the population is above, and the lowermost symbol indicates the lower boundary for 75% of the population (Pennak 1943).

avoidance adaptations (Jensen et al. 1998). When *Chaoborus* were most numerous from 0-2 m at 8 pm, *Daphnia* were most numerous around 9 m (Figure 7). Predation on *Daphnia* is reduced by their migration into the deeper depths at night (Honazato and Dodson 1995); giving reason to why the *Daphnia* of Russell moved to lower depths, thus avoiding the *Chaoborus* that went to the surface.

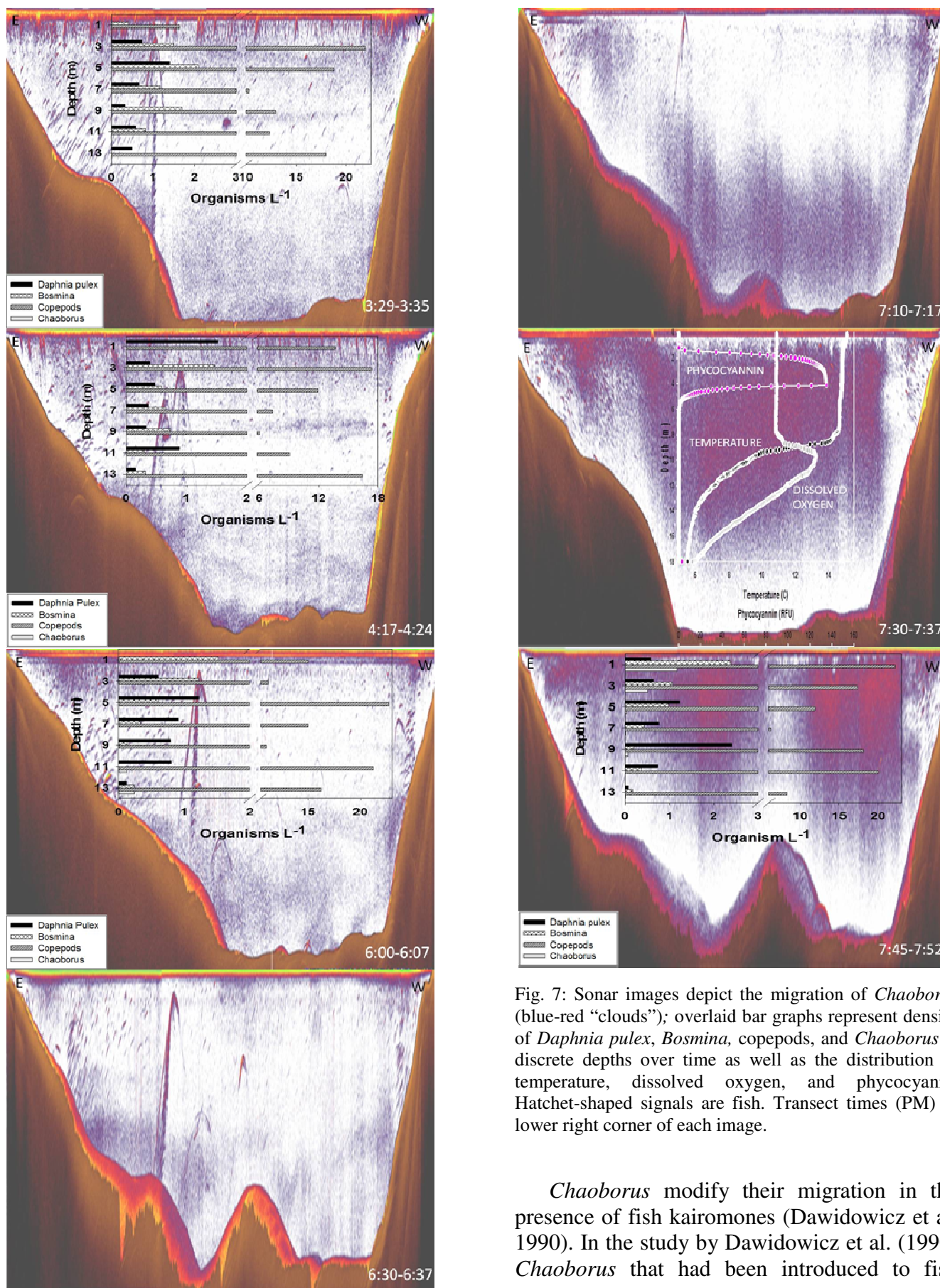


Fig. 7: Sonar images depict the migration of *Chaoborus* (blue-red “clouds”); overlaid bar graphs represent density of *Daphnia pulex*, *Bosmina*, copepods, and *Chaoborus* at discrete depths over time as well as the distribution of temperature, dissolved oxygen, and phycocyanin. Hatchet-shaped signals are fish. Transect times (PM) in lower right corner of each image.

Chaoborus modify their migration in the presence of fish kairomones (Dawidowicz et al. 1990). In the study by Dawidowicz et al. (1990) *Chaoborus* that had been introduced to fish

spent less time in the epilimnion than *Chaoborus* that had not been introduced to fish. The timing pattern of diel vertical migration was similar in the fish introduced and not fish introduced groups, although the fish introduced population remained deeper during the full 24 hours. It was also found that the *Chaoborus* downward movements are triggered by an internal clock, while the movements are adjusted to the presence of light (Haney et al. 1990; Dawidowicz et al. 1990). This could explain why the *Chaoborus* were not seen above 13 m before 6 pm as the sun did not start to set until that time.

The *Bosmina* demonstrated DVM; at 3 pm they were most abundant at 5 m, while at 4-8 pm they were most abundant at 1 m (Figure 7). The *Bosmina* appeared to be migrating to avoid the *Chaoborus* since *Bosmina* can be a food source for *Chaoborus* (Yan et al. 1991). *Bosmina* have been shown to have the tendency to concentrate near the surface to cope with predation pressure (Percicarrari and Rodrigues 2003).

There is no apparent evidence that the calanoid copepods migrated. There were two populations that look to be distinct from one another as one was found between 1-5 m where *Chaoborus* are less numerous and the other between 9-13 m below the most dense region of *Chaoborus*. Migration is not evident as the two populations did not seem to move out of their respective ranges throughout the 3-8 pm time period, and exhibited the same bimodal vertical distribution. It is unclear whether there were two species of copepods using their own unique distribution strategies or one species of copepod using two different strategies.

To further describe the migration of the zooplankton community within Russell Pond more data needs to be collected. The diel vertical migration of the *Chaoborus* had not finished and to capture the end, more sonar graphs would have to be done until all *Chaoborus* rose to the top. The 8 pm sonar showed the majority of the *Chaoborus* population migrating toward the surface, while another population of *Chaoborus* appeared to be

just starting to migrate from the sediments. To follow that, more interactions with fish or other zooplankton may be beneficial to look into to explain why the *Chaoborus* may migrate in two separate waves if that does occur.

The interaction between *Chaoborus*, *Daphnia*, and *Bosmina*, is also unclear. More repetitions of sonar for longer periods of time with more zooplankton counts may explain how they are either affecting or not affecting their respective migrations. Determining what species of fish are present within the lake could give more information on the mechanism behind the *Chaoborus* migration and how that subsequently affects the zooplankton community.

In conclusion the diel vertical migration of the *Chaoborus* was described through sonar and zooplankton samples by depth. From the sonar traces, it appears *Chaoborus* larvae begin moving out of the sediments in the early afternoon, but do not begin the vertical migration into the surface waters until after 6 pm, continuing to migrate after 8 pm. This pattern is similar to that seen with sonar in Barbadoes Pond, a small eutrophic lake (Haney et al. 1990). A second wave of *Chaoborus* migration may occur after 8 pm, but more sonar graphs are needed to determine whether that is true and to what extent. *Daphnia pulex* migrated downward which might serve to minimize predation by *Chaoborus* as they migrated to the surface (Dodson 1988). *Bosmina* migrated toward the surface of the lake indicated by their high abundance from 0-2 m at 8 pm. Calanoid copepods do not appear to migrate but are present in large numbers and may serve as a food source for the *Chaoborus* (Yan et al. 1991). The copepods may also not need to migrate as they are generally more successful than cladocerans in avoiding predation pressure by swimming speed (Percicarrari and Rodrigues 2003). Further studies are needed during different seasons to determine whether the observed migration strategies persist throughout the year.

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Appendix

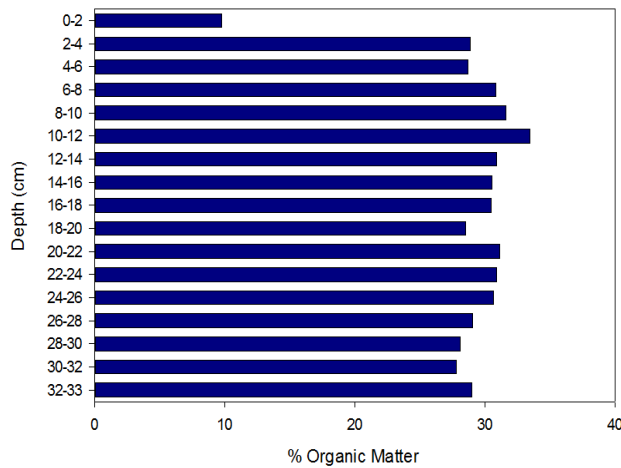


Fig. 9: Sediment core percent organic matter per every 2 cm of core.

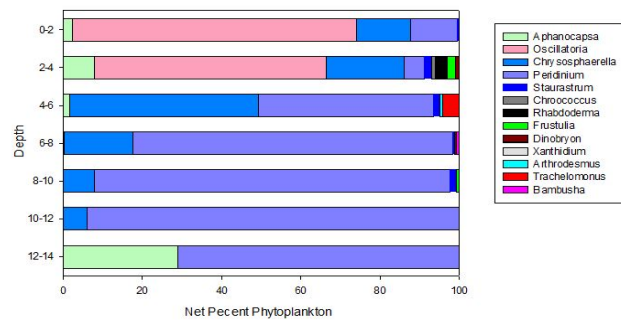


Fig. 10: Net percent phytoplankton as it relates to depth broken down by family.