Dynamics of Supralittoral Freshwater Rock Pools in the Gulf of Maine

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Abstract

Appledore Island, located six miles off the coast of Portsmouth, NH, has over 500 freshwater peripheral pools situated above the intertidal zone and range in size from semi permanent pools measuring 15 centimeters across to larger permanent pools up to about 10m diameter. Seventy eight pools were physically monitored once every four days from June to August 2006 and have provided us with a deeper understanding on dynamics of pond community organization and how organisms cope with rapid and major physical changes. Pools were monitored for temperature, conductivity, pH, dissolved oxygen, water color and clarity, and presence or absence of key macrofauna. The color and clarity of pools, which we used as a proxy for phytoplankton levels, varied throughout the summer and ranged between being always opaque to always clear, or cycling between these two states. Cycling of pools is important for the macrofauna because it indicates varying conditions that organisms must contend with. Clear pools had significantly lower dissolved oxygen levels, pH values and presumably, based on water clarity, lower phytoplankton stocks, while opaque pools had higher levels of both dissolved oxygen and pH and usually very high phytoplankton levels. Diel vertical migration by *Daphnia. pulex* was observed in these island pools which is interesting because of the lack of vertebrate predators. Significantly higher densities of *D. pulex* occurred in the top 10cm during the night than day. With the absence of significant predators, physical or genetic factors must explain the observed migration to the surface at night by *D. pulex*.

Introduction

Trophic cascades are well known to be important in structuring communities. Large ecosystems such as kelp forests as well as eutrophication in large lakes and rivers have been a focus of investigating trophic interactions. However, recently there has been a surge in understanding species and physical dynamic interactions in smaller ecosystems such as temporary rock pools (Romanuk and Kolasa, 2001; Romanuk and Kolasa, 2002; Therriault and Kolasa, 2001).

Rockpools are bodies of water that undergo recurrent, variable wet-dry phases that are unpredictable in their time fluctuation, making them what Williams (1997) defines as temporary intermittent pools. Since predatory vertebrates are usually absent, investigating these small ecosystems has the potential to reveal underlying ecological interactions between lower trophic levels and how they are structured based on species-species and physical interactions. The relative small nature of rockpools and few macroscopic constituents make it easier to determine the community structure. For instance, Blaustein et al. (1995) showed the importance of top invertebrate predators such as water boatmen on the community structure of rockpools. Other studies have investigated the community structure of rockpools and found confounding results with regard to predation and species diversity. Studying basic ecology at such a simple level is a key for applying factors to larger ecosystems with more complex trophic cascades.

Shoals Marine Laboratory, located on Appledore Island, 10km off the Coast of Maine, is an ideal place for studying isolated freshwater rockpools (Figures 1 and 2). These pools have been a focus for studies attempting to understand how their biota fluctuates and persists through time (Figure 3). Their abundance and small sizes also

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mean that they can be manipulated in order to examine what factors are driving the changes that are seen.

The rock pools of Appledore are created from rain draining into pockets, crevices and divots in the bed rock, caused by rock variation in topography and structure. Due to the variability in rock structure, pool dimensions [lengths, widths, and depths] vary from centimeters to meters. Drainage from one pool to another pool only occurs after rain events, and is completely dependent on the weather. Except for rare storm events that occur every few years during extreme spring tides when the sea may inundate and scour them (Hengel, 2006), there is no other form of water exchange, making each pool a virtually autonomous ecosystem for most of the summer. The pools progress through summer on a cycle of hydration to evaporation and back again, which greatly affects the pool ecosystems (see e.g., Therriault and Kolasa, 2001).

Since most rockpools are freshwater and small in nature there have been recurring animal groups that seem to take advantage of these vertebrate-less rockpools (Figure 3). These taxa seem to be able to colonize both ephemeral rockpools and more permanent bodies of water. The dominant zooplankton species present within the pools on Appledore include: two cladoceran crustaceans (*Daphnia pulex, Moina macrocopa),* and three insects *(*the water boatman*, Trichocorixa verticalis*, and a Green and a Red Chironomid midge), and three podocopid ostracod crustacean species (Figure 3). Due to this limited zooplankton diversity and variation in which of the taxa will be present, the ecology of each pool tends to be completely distinct and independent from the others. Furthermore, the extreme nature of the pools has produced survival strategies of the

zooplankton species that vary from diapausing egg production (ephippial production) to physical tolerance.

Desiccation is one of the many physical conditions that the flora and fauna have to endure in order to continue to prosper. Desiccation has a major impact on the zooplankton community (Kuo, 2005). It has been observed in some species of ostracods that they can physically tolerate months of desiccation and still recover (Horne 1993), while the cladocerans reproduce asexually until conditions become suboptimal and then sexually reproduce resistant ephippia. Cantrell and Mclacllen (1982) showed that certain species of dipteran larvae are able to survive periods of drought while others are limited to pools with constant hydration periods until metamorphosis. While the species of chironomids in Appledore rockpools has not been determined there is evidence that depth plays an important role in presence of chironomids on Appledore (this study).

The focus of my study was to determine how physical and biotic factors change with time in different rockpools and determine whether physical characteristics of pools predict the biological composition of any given pool. These predictions were attempted by examining correlations between biota present and physical conditions in the pools. I hypothesized that when conditions in the pools became extreme, e.g., desiccated, nutrient poor, or saline, the biota would change based on the physical shifts in the pool. A previous study on Appledore (Kuo, 2005) experimentally determined the food web of the rockpools. This background was vital because we hypothesized that there would be significant correlations between species in the rockpools depending on either top down or bottom up trophic cascade effects.

In this study I also examined whether *Daphnia* undergoes a diel behavioral alteration of depth distribution. I hypothesized that due to physical, biological or genetic factors that, *Daphnia* would alter their position in the water column based on the time of day. Much research has been done on the diel vertical migration (DVM) of mainland populations of cladoceran species, but relatively little has been done with DVM in ephemeral rockpools. However, one study has observed DVM in pools in islands in the Baltic (Ranta and Nuutinen, 1985).

Materials and Methods

Long term monitoring and analysis:

The Shoals Marine Laboratory is located on Appledore Island in the Gulf of Maine (42° 58'N, 70° 37'W). Appledore is one of nine islands in the Isles of Shoals. There are over 500 supralitoral freshwater rock pools dotting the island rocky perimeter just above the high tide zone. A previous study conducted during the summer of 2005 examined forty-nine of these rock pools located in the northwest and northeast parts of the island. During the summer of 2006 we continued monitoring the 49 pools while also incorporating 27 more and the southeast side of the island. Pools were monitored on a 3 day cycle from June 24th to August 16th. Selection of pools was based on previous year's monitoring, and diversity of pools in terms of color, macrofauna, size, and location.

Monitoring started at 8:30am each day and lasted until each pool designated for the day was monitored and photographed, usually around 10:00am. This protocol allowed for consistency of measurements, so that time of day was not a factor in daily pool variability. The physical conditions of the pools measured were: conductivity,

salinity, temperature, pH, dissolved oxygen, and water level change (from permanent

plastic rulers placed within the pools). Presence or absence of macro-invertebrates was

used to characterize the biological community within each pool. Each pool was sampled

for macrofauna by using a special fine-mesh invertebrate sampling net, along with visual

confirmation of biota present. Time of day was recorded as well as weather conditions.

Color and transparency of each pond were visually designated to broad categories

relating to clarity (clear or opaque), algae present (green or brown) and/or visible organic

matter evident in transparent ponds as red to brown due to tannins and other colored

dissolved organic matter (CDOM).

In order to be able to compare pools for statistical analysis, we classified pools as

green [=opaque] or clear and then we lumped pools into those that remained in one state

or the other throughout the sampling period, or changed state during this time. We then

tested the differences between each category for physical and biological factors over

time.

I averaged the data over the whole summer for each pool with animal presence

and pool clarity ranging from 0 (green) to 1 (clear). In analyzing physical and biological

interactions over time I performed a one-way ANOVA (JMP 5.0.1a) for each of the

response variables against each biological and physical factor as well as pool clarity

levels.

Twentyfour hour monitoring

In order to determine hourly fluctuations in physical parameters of the pools, pH,

dissolved oxygen and temperature were monitored in ten separate pools every three hours

through a span of 24 hours (one full day-night cycle). Pools were selected based on opacity, with four pools being clear and six pools being green or opaque.

I performed a one-way ANOVA (JMP 5.0.1a) for each of these response variables overtime. In two analyses, one pond appeared to be an outlier and the analysis was repeated after excluding that sample (see results).

Diel Vertical Migration(DVM) of Daphnia pulex

D. pulex is a common species of cladoceran that inhabits a variety of temporary to permanent ponds. Many *Daphnia spp.* show a diel vertical migration pattern. We attempted to determine whether *D.pulex* exhibited DVM on Appledore by measuring the vertical distribution of *D. pulex* in two larger ponds (4 and 9 meters across) from the pond surface to a depth of 30cm, using a collecting device divided into five, 10cm sections, we sampled the top 30cm. The two pools were sampled for vertical migration, in each, 4 transects were conducted at each time interval in different parts of the pools. Each transect was a half meter long. At the end of the half meter the clear door was shut trapping the animals within their respective boxes, and the sampling apparatus was lifted out of the water, and filtered through the back screen leaving only animals within the boxes. The animals were preserved in a 70% solution of ethanol for later counting. The same transects were done during the day and at night.

I used a multi-level ANOVA to examine the changes in the distribution of *D. pulex* between day and night. The model included time of day, depth in water column, and their interaction as fixed effects, and pond, transect [pond], and date [pond] as

random effects (JMP 5.0.1a). *D. pulex* abundances were transformed [log (x+1)] to produce residuals that were normally distributed with constant variance.

Results

Long Term Monitoring

  Green vs. Clear Pools. In analyzing the five physical characteristics [depth, temperature, conductivity, dissolved oxygen and pH] of each pool, there was no significant difference between green and clear pools with respect to pond depth (p=0.57), temperature (p=0.13), pH (p=0.25) and conductivity (p=0.20). However, there was a significant difference between green and clear pools with respect to dissolved oxygen (p=0.03); green pools had significantly higher dissolved oxygen levels than clear pools.

  Pool Clarity and Animal Associations. Dissolved oxygen was significant (p=0.023) in pool clarity and animal associations; however, pH was not (p=0.104). Nor were pool clarity levels associated with conductivity, depth, or temperature (p=0.30, p=0.48, p=0.123 respectively). While ostracods were positively associated with pool clarity (p=.0001), there was no association between ostracods and other biota abundances within rock pools (*Moina* p=0.1595; *Daphnia* p=0.1518; green chironomids p=0.3499). *Daphnia* presence was also positively correlated with pool clarity (p=0.0001), but interestingly the other common cladoceran, *Moina*, was negatively associated with pool clarity (p=.0085). Water boatmen showed no relationship to pool clarity (p=0.1030), nor were their abundances associated with ostracods or *Moina* (p=0.5433, p=0.0668 respectively). However, water boatmen populations were positively associated with both *Daphnia* and green chironomid populations (p=0.0079, p=0.0001 respectively).

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Animal Presence with respect to Physical Factors of the pools: First, each of the physical factors were tested against each other to eliminate redundancies. The log of conductivity was not significantly correlated with pH, temperature or depth (p=0.6381, p=06023, p=0.5637 respectively). However, log of temperature was significantly correlated with pH (p=0.0339), but not with depth (p=0.1950). Pond depth was not significantly correlated with pH (p=0.9408). I did not compare dissolved oxygen as a physical measurement. Instead, since it was significantly higher in green pools, I used it as a surrogate for the presence of high levels of phytoplankton, which was therefore a biological factor.

Three physical factors were tested for correlations with animal presence: temperature, depth, and conductivity. Water boatmen were positively associated with pond depth (p=0.0041) but not log (temperature) or log (conductivity) (p=0.2862, p=0.6507 respectively). Similarly green chironomids, a mostly benthic invertebrate, were also significantly associated with pond depth (p=0.0271), but not log (temperature) and log (conductivity) (p=0.9216, p=0.8267 respectively). On the other hand, ostracods were negatively associated with log (temperature) (p=0.0178), while they showed no association with pond depth or log (conductivity) (p=0.2527, p=0.1185 respectively). As with ostracods, *Moina* were also positively associated with log (temperature) and log (conductivity) (p=0.0185, p=0.0128 respectively), but not with pond depth (p=0.0931). Conversely *Daphnia* were negatively associated with conductivity (p=0.0171) and positively associated with pond depth (p=0.0001), but showed no association with log (temperature) (p=0.7218).

Twenty four Hour Monitoring

   Temperature: There was no effect between color of pool and temperature

amplitude (ANOVA, *p*=0.8851) or mean temperature (p=0.2429) (Fig 5). However, pool

#348 [a large and fairly deep, consistently green pool, with extensive vegetation and large

upstream drainage] was determined to be a peculiar outlier, and by excluding this pool

there was a significant difference between pond color (p=0.0224) with green pools being

on average cooler than clear pools over a 24 hour cycle.

   pH: Green pools had significantly higher pH amplitudes (mean 2.89) than clear

pools (mean 1.13, ANOVA, p=0.0006) throughout the course of a day (Fig 5). Clear

pools had a marginally insignificant lower pH than green pools (*p*=0.0630). Upon further

analysis pond #14 [a medium-sized, shallow pond with very extensive upstream

drainage] was excluded as an outlier. This one exclusion made the difference in mean pH

between clear and green pools highly significant (*p*=0.0012).

   Dissolved Oxygen [DO]: Daily amplitude fluctuations for dissolved oxygen were

significantly lower for clear pools (mean 9.63) and higher for green pools (mean 19.3,

ANOVA, *p*=0.0005), even though there was no significant difference in mean DO

between green and clear pools overall (ANOVA, *p*=0.1124) (Fig 5).

Diel Vertical Migration [DVM]

   There were significantly higher numbers of *Daphnia* below 10cm depth of the

pools than the top 10 cm (Least Square Means Difference Tukey HSD p<.0001)

throughout a 24 hour period (Fig. 6). Comparing the different depths within the pool and

time of day revealed that densities at the top 10 cm during the day were significantly

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lower than the bottom and middle depths during the day <u>and</u> night (LSMDT p<.0001)

(Fig. 6). However, significantly higher *Daphnia* numbers were found at the top 10cm

during the night than the day (LSMDT p=.0022), which indicates that they show diel

vertical migration (Fig. 6). At night the bottom and middle depths of the pools have

significantly more *Daphnia* than all locations during the day, which suggests that there

were even more individuals below the depths sampled during the day.

Discussion

Pool Dynamics

From the very beginning of my study, observations indicated that the Appledore

rockpools could be categorized into two distinct categories: clear and opaque (either

green or brown). While it is still not completely evident why rockpools separate into

these categories over time, or how and why certain pools fluctuate temporally between

both categories, the presence or absence of concentrated populations of phytoplankton are

the reason for the distinction. Loder et al. (1996) demonstrated that high nutrient inputs,

mainly nitrogen containing compounds, associated with gull rookeries allow for

eutrophication of pools. They also found that ammonia volatilization was so high that

when scrubbed from the air it could add to nitrogen deposition to pools downwind. If

differences in phytoplankton stocks are the cause of green and clear pools it should be

detected over a span of 24 hours in the DO and pH profiles of pools. Loder et al. (1996)

also showed similar results for the hourly DO and pH pool fluctuations for green pools

(Fig. 4). Our results clearly show that phytoplankton are the explanation for the different

clarity categories (Figures 1 and 2). It would be interesting to study the concentrations

of nitrogen bearing compounds in clear pools to determine if concentrations differ

between those found by Loder et al. (1996) in green pools, and could show that low nutrient levels maybe the cause for the low phytoplankton levels in clear pools.

Living in these ephemeral pools requires special adaptations to physical extremes. The daily variance in DO and pH produced by phytoplankton are two extremes that the major macrofauna must be able to tolerate on a daily basis. While clear pools exhibit less dramatic variations in daily DO and pH fluxes there is still a high level of oxygen depletion at night that the macrofauna must endure to survive in these pools. All but one out of ten pools experienced DO levels below 1ppt for at least 3 hours at night, with most experiencing much lower levels for longer periods. However, most of the macrofauna present in these pools are tolerant to some physical extremes, such as desiccation for ostracods (Horne 1993) and salinity tolerance for *Moina* and certain species of *Daphnia* (Kibler unpublished; Galat and Robinson, 1983). Such environmental extremes have also allowed for evolution of more efficient methods for reproduction in ephemeral environments by cladocerans through ephippial production. It is no surprise that these same macrofauna have some mechanism of tolerating low dissolved oxygen as well as extremely high pH levels on a daily basis.

While Appledore Islands rock pools vary on an hourly basis each day, and it is evident from my data that there is a distinct difference between clear and green pools, it is not clear what maintains the distinction between clear and green ponds over an extended period of time, in this case a summer. Some ponds remained in one state or the other, while still others switched from green to clear or from clear to green, or some sometimes switched back and forth. Out of all physical characteristics measured DO is the only one that differed consistently between both green and clear pools. The results

are of particular interest because the data exclude depth as a determining factor between green and clear pools. One would expect that shallower pools would be more eutrophic due to concentration of nutrients and that shallow depth would be correlated with green pools, however this was not the case. This lack of correlation suggests that some other factors are influencing the high phytoplankton levels.

Other possibly important factors in determining the difference between clear and green pools are: drainage size, history of nutrient inputs, location to gull rookeries, and presence/absence of particular macrofauna. While the first three factors could potentially concentrate nutrients and allow for phytoplankton blooms, the macrofauna could act as a top down control and explain the difference between clear and green pools. The most obvious choice for the difference between clear and green pools are nutrients. As discussed earlier in this paper nutrients in both types of pools need more attention.

It was not surprising that depth was positively correlated with water boatmen, green chironomids and *Daphnia*. Green chironomids in particular rely on deeper pools (i.e. has a longer duration of their water mass) in order to have sufficient time to complete their larval stages. Making their protective cocoon out of the benthos material, green chironomids structure the bottom of pools by congealing algae, fecal material and detritus together (Hershey, 1987; Hirabayashi & Wotton, 1999). Water boatmen have been shown to be the top predator in rockpools lacking vertebrates and, since deeper pools apparently have more benthos to scavenge and therefore more prey (Warren, 1989; Pajunen & Salmi, 1991, Kuo Honors Thesis, 2006), it is not surprising that their presence correlates with depth. It could potentially be metabolically costly to move from pool to pool in search of food, therefore by selecting deeper more permanent pools it would

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allow for less pool to pool movement due to the presence of more prey and scavenging opportunities. *Daphnia* correlation with an increase in depth is of particular interest since diel vertical migration was observed in some of the deepest rockpools. It may be that the deeper pools offers more protection to *Daphnia* from ultraviolet radiation and/or are possibly more chemically stable. *Daphnia* individuals are apparently less salt tolerant than *Moina* and therefore may be more restricted in their distributions, which is consistent with a negative correlation between conductivity and presence of *Daphnia* (Kibler Unpublished). If deeper pools tend to be more stable and dilute, this could account for the recurrent observation of *Daphnia* in the larger pools. Ephemerality has been shown to reduce species diversity as well as decrease community variability (Therriault and Kolasa, 2001). Thus, these species appear to be somewhat "constrained" to more permanent pools.

Bottom-up or Top-down?

Since the basic types of pools are known: green and clear, and the biota presence or absence in pools is known, it should be possible to determine which pools are controlled by top down or bottom effects. Cladocerans are known planktivores so *Daphnia* and *Moina* should affect water clarity (Pogozhev & Gerasimova, 2005). Ostracods, on the other hand, are primarily known to be detritivorous or scavengers (Ganning, 1971; Kuo, 2005) so would not be expected to affect water clarity directly. My results are only partly consistent with these expectations: *Daphnia* are associated with water clarity, but *Moina* were not, and, conversely, ostracods were. How can these anomalies occur?

Cladocerans: Under eutrophic conditions with high phytoplankton populations, *Daphnia* can clear pools. As long as *Daphnia* populations remain stable they can significantly filter a pool, especially since filtering rates increase with temperature and some of these pools reach higher temperatures than 25°C (Burns, 1969; Porter et al., 1983) . These zooplankton can actively "de-eutrophicate" lakes with high nutrient levels, which results in an increase in water transparency (Pogozhev and Gerasimova, 2005) and could be what is occurring in the Appledore rockpool systems. Pools start off green with high amounts of nutrients and once ephippia hatch the numbers of *Daphnia* increase and filter the pool until it transitions from green to clear. How long this process takes is unknown, especially in ephemeral pools. Since these pools are more dynamic than more permanent bodies of water, *Daphnia* populations might not survive a bout of high temperatures or excessively low DO levels, which has been shown to reduce filtering rates of water (Gliwicz, 1990). There is the potential to not see a transparency transition. Instead there would be low populations of cladocerans unable to adapt to the excessively extreme conditions and would eventually die-off leaving the pool green.

While there is evidence for *Daphnia* acting as top-down control within the rockpools there is evidence that the opposite is true with *Moina*. Surprisingly, *Moina* are positively associated with green pools, which suggests that there might be bottom-up control by the *Moina*. *Moina* might be controlled by the level of phytoplankton present. I observed that high concentrations of *Moina* usually resulted in population crashes and subsequent transitions of pools from clear to green (Levas personal observation). On the other hand I observed that high levels of *Daphnia* concentration did not always lead to crashes and pool transitions. This difference between these two cladocerans could be the

result of different levels of reproduction as well as differing ability to handle high density levels of conspecifics but low levels of food. *Daphnia* have been shown to reduce their feeding rates under such conditions (Helgen, 1987), which could potentially benefit the *Daphnia* by reducing energetic cost of filtration and instead conserving energy under low food conditions. Research done by Bradley et al. (1991) showed that when daphnids experienced prolonged times of starvation, maintenance and growth where supported by stored sources, but reproduction immediately ceased. *Daphnia* and *Moina* have been shown to store lipids similarly (Macedo & Pinto-Coehlo, 2001), which leads to the question of how the metabolism of the two cladocerans differs under starvation conditions. If *Daphnia* control the level of phytoplankton in a pool and are able to sustain periods of low food abundance and *Moina* on the other hand cannot and are dependent on high levels of phytoplankton, this difference could explain the presence of both top- down control by *Daphnia* and bottom up control of phytoplankton on *Moina.*

Ostracods: Surprisingly, ostracods were positively correlated with clear pools, so it might be expected that they too would exert top down control in the pools where they are present. Ostracods, however, are mostly detritivores and scavengers, but occasionally predators (Ganning, 1971; Kuo, 2005) so this relationship might be indirect. Oddly, especially *Daphnia* [and also *Moina*] populations where not correlated with ostracod presence, which is surprising because if it is a top down control by the ostracods, there should be some correlation between prey species, assuming they prey upon cladocerans as Kuo (2005) suggests. However, since ostracods are scavengers as well as predators there is the indirect possibility that after *Moina* and *Daphnia* populations crash ostracod populations infiltrate and consume the carrion. By consuming the carrion they reduce the

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decomposition load on a pool, thereby reducing nutrients, particularly nitrogen, which has been associated with eutrophication in rockpools (Loder et al., 1996). Conversely, it may be more likely that ostracod scavenging is associated with some other factors such as drainage size or locality in relation to gull rookeries, which contributes to a pool being clear and having less phytoplankton than a green pool (Loder et al., 1996).

The top predators of the Appledore rockpool systems and other vertebrate-free rockpool systems are adult water boatmen (Kuo, 2005; Warren, 1989; Pajunen & Salmi, 1991). My data showed that water boatmen were positively correlated with green chironomids, *Daphnia* and to some extent *Moina*, but not ostracods. Since water boatmen are not correlated with pool clarity, and since they are known predators of planktivorous cladocerans (Kuo, 2005), it makes sense that they would be associated with *Daphnia* and *Moina*, which could result in a top-down effect. The lower trophic levels, in this case cladocerans, as well as green chironomid larvae, affect the presence of water boatmen. Since water boatmen are able to move from pool to pool through flight (ref), this ability may play an important role in their distribution across pools. To survive they must occur with their prey so it would be to their benefit to be able to "track" their prey from pool to pool. Thus, the presence of cladocerans as well as green chironomids may determine the presence of water boatmen. A similar study determined that there was top down control by a backswimmer, a comparable predator, and the correlations between primary prey and predator were negative (Blaustein et al, 1995).

Kuo (2005) experimentally analyzed the complex food web structure of these ponds and she found that green chironomids were mostly scavengers but also predators to some extent. While green chironomids are a significant part of the rockpools, the benthos

was not regularly sampled in my study so I have no good evidence of their effect on the pools.

The trophic structure of these pools is extremely complex. It seems that there are a multitude of factors that interact to produce unique rock pool ecosystems even among nearby pools. Nutrients must play some factor in determining how the phytoplankton stock will be able to thrive as well as the presence or absence of cladocerans. Since water boatmen are able to move from pool to pool independently of rain events, they add complexity to the question of whether or not these pools are dominated by top-down or bottom-up control. Another year of research along with nutrient data should explain the true driving forces within these dynamic ecosystems.

Diel Vertical Migration (DVM)

Diurnal Vertical Migration (DVM) has been widely observed to occur in species of *Daphnia* worldwide. In the only other study that has examined DVM in *Daphnia* in rock pools, Ranta and Nuutinen (1985) also found it to occur, which suggests that predation not the sole driving force in DVM exhibited by zooplankton. Other studies have established that other factors such as ultraviolet radiation avoidance (Kerfoot, 1985; Leech and Williamson, 2001; Rhodes et al. 2001) and food abundance (Johnsen and Jakobsen, 1987) play some role in DVM.

The pools sampled in my study only reach maximum of about a meter depth, which contrasts with larger lakes where the migration can be many meters and has been positively associated with predation. *Daphnia* on Appledore are not under predation

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pressure from vertebrates so the predation pressure hypothesis does not directly explain the observed DVM.

Experiments done by Leech and Williamson (2000) and Rhodes et al. (2001) have shown that *Daphnia* will avoid UV by exhibiting DVM. Due to the shallow nature of the Appledore rock pools (less than 1 meter) UV avoidance is a plausible direct cause for DVM. Phototaxsis has long been established to affect *Daphnia* vertical migration (Ringelberg, 1964), and increased light intensity causes greater DVM (Ringelberg and Flik, 1994). If UV is an explanation for the observed DVM it would be interesting to test whether dissolved organic matter within the pools aids in UV protection and therefore modulates DVM.

Other physical factors along with food depletion could also contribute to the observed DVM. For instance, not only could avoidance of UV during the day be an effect, oxygen depletion at night and/or better opportunities for grazing could combine to influence the observed DVM. Johnsen and Jakobsen (1987) established that low levels of food cause *Daphnia* to take higher risks and forage during the day. Therefore, food limitations could breakdown DVM because *Daphnia* would be forced to forage in surface waters. If avoiding UV keeps *Daphnia* at depth by day, phytoplankton stocks could increase during the day at the surface, thus altering food stock availability. However, the pools monitored for DVM were not green and were relatively transparent, which suggests that *Daphnia* were keeping the phytoplankton stocks consistently low but still demonstrated DVM.

Finally genetic effects could be another explanation for the observed DVM (Weider, 1984). If the Appledore populations show residual genetic effects for DVM to

avoid predators and have sufficient gene flow with predator-subjected populations on the mainland, then predator avoidance behavior might persist even in the absence of predators. King and Miracle (1995) demonstrated that two separate clone types of *Daphnia* undergo differing depths of DVM suggesting that the behavior is genetically regulated. Thus, on Appledore, if the clones and the ephippia have kept some gene that encodes for DVM, this could explain the variance in surface populations between day and night. Since we now that we know that DVM occurs in Appledore populations, it would be interesting to test the cause of DVM experimentally through, food, light and potentially DO manipulations and determine which factors are controlling DVM in *Daphnia* on Appledore.

References

Bazzanti M., M. Seminara & Tamorri, C. 1989. A note on chironomid (diptera) of temporary pools in the National Park of Circeo, Central Italy. Aquatic Ecology. 23: 189-193.

Blaustein L., B.P. Kotler & Ward, D. 1995. Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. Ecological Entomology. 20: 311-318.

Bradley, M.C., Perrin, N., & Calow, P. 1991. Energy allocation in the cladoceran *Daphnia Magna* Straus, under starvation and refeeding. Oecologia. 86: 414-418.

Burns, C.W. 1969. Relation between filtering rate, temperature, and body size in four species of Daphnia. Limnology and Oceanography. 14: 693-700.

Cantrell, M. A. & McLachlan, A. J. 1982. Habitat duration and dipteran larvae in tropical rain pools. Oikos. 38: 343-348.

Galat, D.L., & Robinson, R. 1983. Predicted effects of increasing salinity on the crustacean zooplankton community of Pyramid Lake, Nevada. Hydrobiologia. 105 : 115-131.

Ganning B., 1971. On the ecology of *Heterocypris salinus, H. incongruens* and *Cypridopsis aculeata* (Crustacea: Ostracoda) from Baltic brackish-water rockpools. Marine Biology 8: 271-279.

Gliwicz, M.Z. 1990. Why do clodocerans fail to control algal blooms? Hydrobiologia. 200-201: 83-97.

Helgen, G.C. 1987. Feeding rate inhibition in crowded *Daphnia pulex*. Hydrobiologia. 154: 113-119.

Hengel, K. 2006. The spatial and temporal dynamics of supra-littoral rock pools on Appledore Island, Maine, and the swarming behavior of the cladoceran crustacean *Moina macrocopa.* Undergraduate Senior Honors Thesis, Cornell University; 53 pp.

Hershey A.E., 1987. Tubes and foraging behavior in larval Chironomidae: implications for predator avoidance. Oecologia 73:236-241.

Hirabayashi K .& R.S. Wotton, 1999. Organic matter processing by chironomid larvae (Diptera: Chironomidae). Hydrobiologia 382: 151–159.

Horne, F.R. 1993. Survival strategy to escape dessication in a freshwater ostracoid. Crustaceana. 65: 53-61.

Johnson, G. H. and Jakobsen, J. 1987. The effect of food limitation on vertical migration in *Daphnia longispina.* Limnology and Oceanography. 32: 873-880.

Kerfoot, W.C. 1985. Adaptive value of vertical migration: Comments on the predation hypothesis and some alternatives. Contribution Marine Science. 27: 91-113.

King, C.E., and Miracle, M.R. 1995. Diel vertical migration by *Daphnia longispina* in a Spanish lake: Genetic sources of distributional variation. Limnology and Oceanography. 40: 226-231.

Kuo, S.L. 2005. Food web interactions in supratidal freshwater rock pools in the Gulf of Maine. Undergraduate Biology Honors Thesis, Cornell University; 31pp.

Leech, D.I. and Williamson, C. E. 2001. In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia.* Limnology and Oceanography. 46: 416-420.

Loder, T.C., Ganning, B., Love, J.A. 1996. Ammonia nitrogen dynamics in coastal rockpools affected by gull guano. Journal of Experimental Marine Biology and Ecology 196: 113-129.

Macedo, C.F. & Pinto-Corlho, R.M. 2001. Nutritional status response of *Daphnia laevis* and *Moina micura* from a tropical reservoir to different algal diets: *Scenedesmus quadricauda* and *Ankistrodesmus gracilis*. Brazilian Journal of Biology. 61.

Pajunen V.I. & J. Salmi, 1991. The influence of corixids on the bottom fauna of rock-pools. Hydrobiologia 222: 77-84.

Pogozhev, P.I. & Gerasimova, T.N. 2005. The role of filtering zooplankton in de-eutrophication of water bodies. Water Resources. 32: 337-345.

Porter, K.G., Feig, Y.S., & Vetter, E.F. 1983. Morphology, flow regimes and filtering rates of *Daphnia, Ceriodaphnia,* and *Bosmina* fed natural bacteria. Oecologia. 58: 156-163.

Ranta, E. & Nuutinen, V. 1985. Daphnia exhibit diurnal vertical migration in shallow rock pools. Hydrobiologia. 127: 253-256.

Rhode, S.C., Pawlowski, M., and Tollrian, R. 2001. The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. Nature. 412: 69-72.

Ringelberg, J. 1964. The positively phototactic reaction of *Daphnia magna* Staus: A contribution to the understanding of diurnal vertical migration. Netherlands Journal of Sea Research. 2: 841-847.

Ringleberg, J. and Flik, B.J.G. 1994. Increased phototaxis in the field leads to enhanced diel vertical migration. Limnology and Oceanography. 39: 1855-1864

Romanuk, T. N. & Kolasa, J. 2001. Simplifying the complexity of temporal diversity dynamics: a differentiation approach. Ecoscience. 8: 259-263.

Romanuk, T. N. & Kolasa, J. 2002. Environmental variability alters the relationship

    between richness and variability of community abundances in aquatic rock pool

    microcosms. Ecoscience. 9: 55-62.

Therriault, T. W. & Kolasa, J. 2001. Desiccation frequency reduces species diversity and

    predictability of community structure in coastal rock pools. Israel Journal of

    Zoology. 47: 477-489.

Warren, P.H., 1989. Spatial and temporal variation in the structure of a freshwater food

    web. Oikos 55: 299-311.

Weider, L.J. 1984. Spatial heterogeneity of *Daphnia* genotypes: Vertical migration and

    habitat partitioning. Limnology and Oceanography. 29: 225-235.

Williams, D.D. 1997. Temporary ponds and their invertebrate communities. Aquatic

    Conservation: Marine and Freshwater Ecosystems. 7: 105-117.

Figures

Figure 1. This picture illustrates the difference between two pools that are extremely close to each other yet visibly different in terms of opacity. Pool 110 is located on the right and is green opaque, while pool 111 is located on the left and has a clear tannin color.

Figure 2. These pictures demonstrate the difference a pool (348) can experience over the summer. The first picture was taken on June 13th, 2006 while the second picture was taken August 10th, 2006.

Figure 3. Top- Red chironomid. Mid-Right-*Moina Macrocopa*. Mid-Left-Ostracod spp.
Bot-Right-*Daphnia pulex.* Bot-Left-Waterboatmen

Hourly pH Profile for two Pools
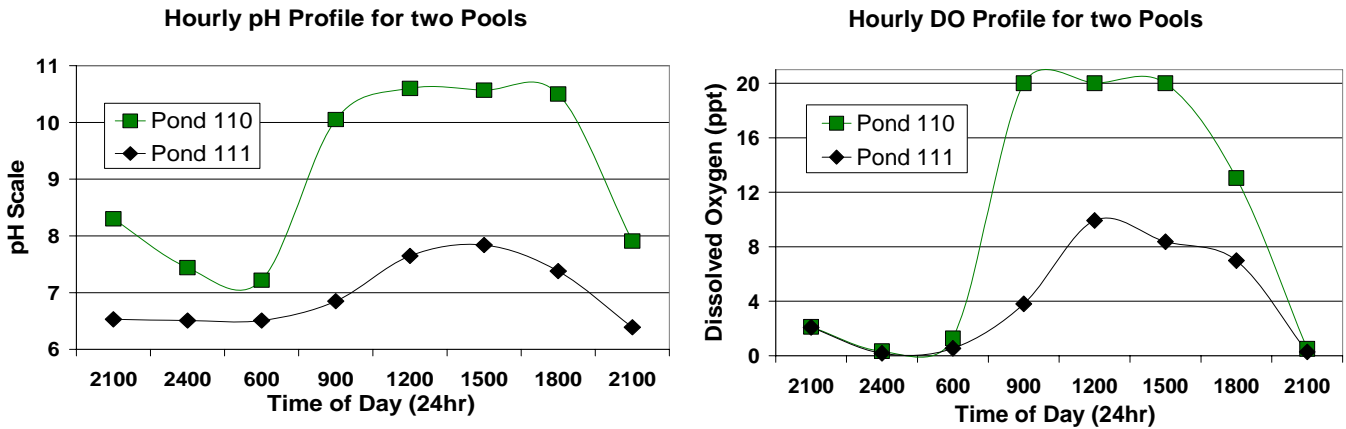

Hourly DO Profile for two Pools

Figure 4. Represented in this figure are the individuale pH and Dissolved Oxygen profiles for two separate pools that can be seen in Figure 1. Pond 110 is characterized as a green pond while pond 111 is clasified as a clear pond.

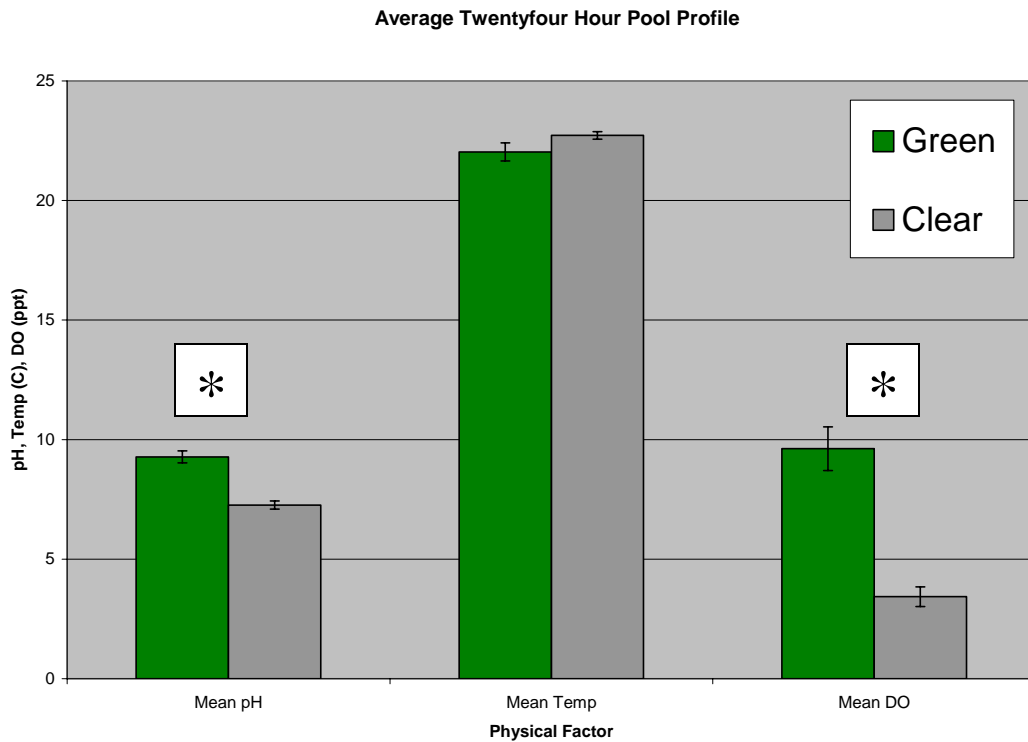**Average Twentyfour Hour Pool Profile**

Figure 5. This graph shows the average pH, temperature, and DO for pools sampled over a 24 hour period with standard error bars. The * denotes significant difference between green and clear pool types.
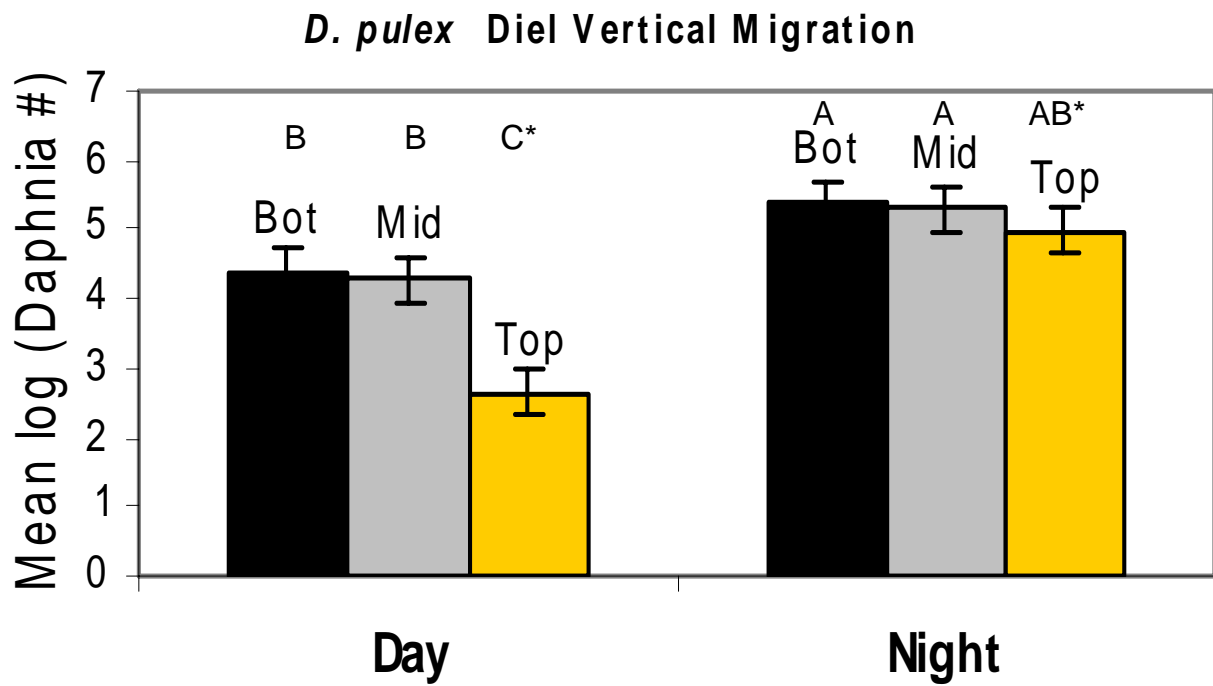
D. pulex Diel Vertical Migration

Figure 6. Shows the distribution of Daphnia in the top 30cm of pools sampled during night and day.