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Spatial Heterogeneity of Ecosystem Metabolism in a Shallow Wetland

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ABSTRACT

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Spatial heterogeneity in ecosystem metabolism may play a critical role in determining ecosystem functions. Variation in ecosystem metabolism between macrophyte patches in shallow wetlands at the extremes of freshwater habitats has not been investigated. We estimated ecosystem metabolism in mesocosms containing different macrophytes using 24-hour oxygen curves to test our hypotheses: (1) net aquatic production (NAP) during spring and summer would be similar among algal patches (metaphyton and *Chara*), (2) NAP in algal patches would be greater than patches dominated by the vascular plant *Potamogeton foliosus*, (3) heterotrophy and anaerobiosis would be greatest in patches dominated by *Lemna*, and (4) the pond would be autotrophic in the spring and fall but heterotrophic in the summer. We found that different patches generated differences in NAP but not always as we predicted. NAP was different among algal patches in the spring and summer, and only metaphyton was more heterotrophic than *P. foliosus*. In the summer *Chara* and *Lemna* patches were heterotrophic and metaphyton became autotrophic. As predicted, the pond was net autotrophic in the spring and heterotrophic in the summer with an absence of patchiness in fall attributed to the dominance of *Lemna*. This research suggests the importance of macrophyte patchiness in wetlands in determining patterns of ecosystem metabolism despite challenges in measuring 24 hour oxygen curves (e.g. oxygen supersaturation). Consequently, macrophyte traits may be important in determining spatial heterogeneity of ecosystem metabolism in shallow ponds.

Keywords: ecosystem metabolism, wetlands, diel oxygen, primary production, respiration, GPP, NAP, *Chara, Potomogeton foliosus,* metaphyton, *Lemna,* autotrophic, heterotrophic, hypoxia, Hobble Creek, submersed macrophytes

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INTRODUCTION

Odum (1956) describes ecosystem metabolism as the balance between energy fixed (gross primary production) and energy consumed (community respiration). In aquatic environments ecosystem metabolism is used to track the flow and storage of carbon and nutrients, to distinguish autotrophic from heterotrophic conditions, and to determine the importance of allochthonous versus autochthonous energy inputs (Cronk and Mitsch. 1994, Cole et al. 2000, Staehr et al. 2012, Jankowski et al. 2014). It is also used to monitor how humans alter aquatic resources (Bernot and Wilson 2012, Vaquer-Sunyer et al. 2012), and to evaluate the effectiveness of habitat restoration projects (Espanol et al. 2013).

Gradients in water depth and flow define shallow wetlands, lakes, wadeable streams, and rivers (e.g. Dodds and Whiles 2010). Most studies on ecosystem metabolism in the freshwater environment have been conducted in lakes, streams and rivers (Hanson et al. 2008, Dodds et al. 2013, Hoellein et al. 2013). Ecosystem metabolism has rarely been measured in wetlands (Christianson et al. 2013), especially small, stagnant ponds at the extreme end of the depth and flow continuums.

Recent technological advancements have increased the use of 24-hour oxygen curves in estimating ecosystem metabolism in freshwaters (Staehr et al. 2012). Wetlands present unique challenges to measuring ecosystem metabolism because of high spatial variation in oxygen concentrations over short distances (decimeters). High spatial variation in oxygen is

characteristic of poorly mixed systems (e.g. Rader and Richardson 1992). Mixing of water is minimal in small wetlands with a short fetch because of the absence of currents and a reduction in wind (Wetzel 2001). In lakes, habitats that produce and consume oxygen at different rates (e.g. open water versus littoral zone) generate considerable spatial heterogeneity in metabolism (Coloso et al. 2008). Spatial heterogeneity in ecosystem metabolism in poorly mixed wetlands may be generated at much smaller scales due to variation in vegetation communities.

Aquatic macrophytes form distinct patches in wetlands (Wetzel 2001), which may be important in determining spatial heterogeneity in ecosystem metabolism. For example, net ecosystem production (NEP) in natural and constructed riparian ponds in Spain was greater in patches dominated by *Chara* than in patches dominated by *Typha* or *Phragmites* (Espanol et al. 2013). Similarly, Christianson (2013) found that *Chara* had strong effects on the metabolism of an oligotrophic pond in Sweden. Also, gross primary production (GPP) in the Everglades was highest where algal periphyton dominated production and lowest in patches dominated by the emergent macrophyte, *Cladium* (Hagerthey et al. 2010). These studies suggest a distinction between vascular plants and algae. For example, using lacunar spaces oxygen will diffuse to the roots of vascular macrophytes (emergent and submersed) where it prevents the toxic effects of anaerobic respiration (e.g. Armstrong et al. 1978, Mermillod-Blondin et al. 2008). Consequently, part of the oxygen produced by photosynthesis does not diffuse into the water but enters the soil (e.g. Wetzel 2001). However, oxygen generated by algae will readily diffuse into the water

because they have no vascular tissue (e.g. Irwin and Davenport 2002). Thus, patches dominated by algae should have higher oxygen concentrations than patches dominated by vascular macrophytes if community respiration is similar.

Algal assemblages are often abundant in small, stagnant ponds (Dodds 1991, Scheffer et al. 1997). Goldsborough and Robinson (1996) outline the factors producing four stable states of algae in wetlands (epipelon, epiphyton, phytoplankton, and metaphyton). Macroscopic, floating tufts of filamentous algae (metaphyton) are characteristic of sheltered wetlands with high nutrients, high irradiance, and a stable water column (Spivak et al. 2011). Recent studies show that mats of floating vascular macrophytes (pleustophyton) can flourish under the same conditions as metaphyton (Pokorny and Rejmankova 1983, Scheffer et al 2003). Thus, it appears that there are two stable states under the same set of environmental conditions (Smith 2012, Scheffer et al. 1997). Both types of patches can have strong effects on oxygen availability and consequently aquatic net primary production (Bott et al. 2012, Goodwin et al. 2008, Pinardi et al. 2011).

Our objective was to experimentally determine the effects of macrophyte patchiness on ecosystem metabolism and oxygen dynamics using mesocosms in a sheltered, riparian pond. This pond was not shaded, had a stable water column, and had high levels of nutrients because of its near proximity to an urban area. Our hypotheses reflected the successional sequence of macrophytes over the growing season: 1) net production in the water column during spring and

summer would be similar in two types of algal patches (metaphyton and *Chara*), 2) net production in the spring and summer of both algal patches would be greater than patches dominated by a submersed vascular macrophyte (*Potamogeton foliosus*), 3) heterotrophy and anaerobiosis in the summer would be greater in patches dominated by pleustophyton (*Lemna*) than in either of the algal patches (*Chara* and metaphyton), and 4) this pond would be autotrophic in the spring and fall but heterotrophic in the summer because heterotrophic respiration would become increasingly important at warm temperatures.

METHODS

Site Description

The Hobble Creek Wildlife Management Area is comprised of constructed wetland ponds just upstream from the confluence of Hobble Creek and Utah Lake, Utah, USA (40° 11' 4.35" N; 111° 39' 1.19" W). The ponds were created in the summer of 2009 in the floodplain of Hobble Creek, which originates in the Wasatch Mountains and flows through an urban area before draining into the lake. Utah Lake is a large (380 km^2), shallow (average depth 3.2 m), eutrophic lake in central Utah. We chose a small (323 m^2) shallow (0.3 m to 0.6 m) permanent pond at 1372 m asl for our study. Groundwater seepage likely sustains the pond during the hot summer months. On an average water year it may be inundated by Hobble Creek during spring runoff, but can also become part of the Utah Lake littoral zone during years with an unusually high snow pack. All of the ponds and the entire floodplain were planted with native aquatic and semi-

aquatic vascular plants, whereas all submersed and floating vegetation was left to colonize and develop on its own.

The margin of the pond consisted of a narrow strip of *Typha latifolia* and *Juncus balticus*. They occurred above the water line for most of the growing season and thus, were not included in our estimates of ecosystem metabolism. In the spring of 2013 metaphyton, *P. foliosus,* and *Chara* grew quickly, each forming distinct patches that covered about one third of the pond by late May. *Lemna* began to grow in June, and covered about 25% of the pond in sparse patches by July. In July, *Chara* and metaphyton patches continued to expand although some of the metaphyton began to senesce, whereas *P. foliosus* had declined to just a few small patches. By September, the pond was covered with *Lemna.* Metaphyton and *Chara* were reduced to a few small patches, and *P. foliosus* had completely died-back. Qualitative observations suggest that this general successional sequence was common in these ponds, except for the dominance of *Lemna* late in the growing season, which varied from pond to pond and from year to year in the same pond.

Metaphyton was primarily a mixture of chlorophyte filaments (*Spirogyra* spp., *Cladophora* spp., and *Mougeotia* spp.), filamentous cyanophytes (*Oscillatoria* spp.), and a diverse assemblage of epiphytic diatoms common in the great basin (Keleher and Rader 2008). This pond was also inhabited by an assemblage of typical wetland macroinvertebrates (e.g. Corixidae, Notonectidae, Chironomidae) and a single species of fish, *Gambusia affinis*.

Macrophyte Spatial Heterogeneity

We deployed multiparameter parameter sondes with optical oxygen sensors (EXO2, Yellow Spring Instruments) in three replicate mesocosms in each of three macrophyte treatments in the spring (*P. foliosus*, *Chara*, and green metaphyton), two replicates in four treatments in the summer (*Chara*, green metaphyton, brown metaphyton, and *Lemna*) and three replicates in one treatment in the fall (*Lemna*). The brown metaphyton consisted of senescent metaphyton that was noticeably deteriorated. We also positioned a single sonde in each treatment patch in all three seasons as a "cageless" control. Oxygen sondes recorded oxygen concentration (mg L^{-1}), temperature (C), and pH every five minutes for 72 hours from 3 - 6 June, 22 - 25 July, and from 27 - 30 September 2013 with a margin of error of 1% O_2 saturation between 0-200% and 15% O_2 saturation above 200%. Macrophyte ash-free mass was measured for all mesocosms at the end of each 72-hour period because oxygen evolution and metabolism may depend on macrophyte abundance. These samples were dried at 50 °C for 24 hours and ashed at 500 °C for 60 minutes (Steinman et al. 2006). We made no attempt to separate the effects of epiphytic algae from the dominant macrophyte in each treatment.

Each mesocosm was constructed of clear corrugated greenhouse roofing with >95% light transmission. They were cylindrical in shape (80 cm diameter), open at the top, and pushed into the sediment to seal out the effects of nearby patches of a different type. Mesocosms were allowed to settle for several hours before measurements began and were removed at the end of each 72-

hour period. All sondes were suspended from poles over the top of each mesocosm so that the sensor was positioned equidistant from the surface of the water and the sediment. All sondes were calibrated immediately prior to each sampling period according to manufacturer recommendations. One sonde failed to record data at high concentrations of oxygen; these data were estimated from the model using interpolation. In order to determine the spatial variation of oxygen in our mesocosms, we collected three measurements at points on an equilateral triangle (40 cm on each side) at the same depth as our oxygen sonde during the summer with a handheld optical oxygen sensor (ProODO, Yellow Springs Instruments) in a total of seven mesocosms with at least one selected from each treatment.

We used a mixed model analysis of variance (ANOVA) with a Kenward-Roger adjustment for small sample sizes (Kenward and Roger 1997) implemented using the MIXED procedure in SAS 9.3 (SAS Institute, Cary, NC) to test for differences in NAP between macrophytes types after verifying parametric assumptions. For diel oxygen measurements in aquatic systems, it is necessary to distinguish NAP from total NPP (e.g. Hagerthey et al 2010). NAP applies to submersed primary producers that release oxygen into the water (e.g. *Chara* and metaphyton), whereas NPP includes macrophytes that release oxygen directly into the atmosphere (e.g. emergent macrophytes). Positive or negative values of NAP indicated autotrophic versus heterotrophic conditions within our mesocosms, respectively.

Treatments of aquatic macrophytes and season were fixed categorical variables, whereas random effects were time (days in each 72-hour period) and mesocosms. We compared least squares means of NAP in the spring and summer between metaphyton patches versus *Chara* patches to test hypothesis 1, metaphyton patches versus *P. foliosus* patches and *Chara* patches versus *P. foliosus* patches for hypothesis 2), and metaphyton patches versus *Lemna* patches and *Chara* patches versus *Lemna* patches to test hypothesis 3. Abnormal variation in oxygen at unusual times of the day indicated that some of the "cageless" treatments were likely contaminated by human intrusion (substrate disturbance). Thus, all "cageless" treatments were dropped from the analysis. Biomass of macrophytes was also dropped from the final analysis because it had no significant effect on NAP.

Physical and Chemical Parameters

Total solar irradiance (W m^{-2}) was recorded every five minutes with a pyranometer (SP-212, Apogee Instruments) mounted in the open on a 1.8 m pole for each 72-hour period. In addition to our sonde data (oxygen, conductivity and pH), we collected six water samples in two randomly chosen mesocosms per treatment during each season to determine the concentrations of fluoride, chloride, sulfate, bicarbonate, total nitrogen, total organic carbon, and total phosphorus. One sample was collected just before dawn (6:00 am) at lowest oxygen concentrations and one at peak photosynthesis (2:00 pm). These samples were immediately acid

stabilized and placed on ice before analysis by the BYU- Environmental Analytical Lab (College of Life Sciences Plant and Wildlife Department, Provo Utah).

Metabolism calculations

We modified standard equations (see Staehr et al. 2010) to calculate ecosystem metabolism in our mesocosms:

$$NAP = GPP - ER \pm F - A \text{ where,}$$

NAP ($\Delta O_2/\Delta t$) is net aquatic production in the water column, GPP is gross primary production, ER is ecosystem respiration, and F is the gas flux attributed to atmospheric diffusion and aeration. "A" includes all other factors that may be relevant in a specific body of water (e.g. salinity). NAP is the sum of the change in dissolved oxygen concentration between each 5 minute measurement over a 24-hour period (GPP) after subtracting losses attributed to ER. ER is based on the nighttime decline of oxygen after accounting for the diffusion rate (F), which is small in sheltered wetlands. "F" (g O_2 m^{-2} h^{-1}) is a function of the piston velocity (k) multiplied by oxygen saturation and was recalculated each time oxygen was recorded (Hotchkiss and Hall 2014):

$$F = k\,(O_{2meas} - O_{2sat}) \text{ where,}$$

O_{2meas} represents the recorded concentration (mg L^{-1}) and O_{2sat} (mg L^{-1}) corresponds to 100% saturation based on water temperature, salinity, and barometric pressure for each 5 minute

interval. "k" (m h^{-1}) represents the effects of water viscosity, wind, and temperature on "F" (Staehr et al. 2010):

$$k = k_{600} \times ([Sc/600]^{-0.67}) \text{ where,}$$

"k_{600}" was the average nighttime slope for each 24-hour oxygen curve in a season (e.g. Cole et al. 2000, Jähne et al. 1987). "k_{600}" was multiplied by the water viscosity (represented by the Schmidt (Sc) number) with an exponent of -0.67. Wetlands have a lower exponent than streams and lakes (-0.5) because diffusion across the air-water interface is slower in a stagnant body of water (Jähne 1998). All calculations were done in R (R Development Core Team 2012). The units of each term were expressed as g O_2 m^{-2} h^{-1}.

Light inhibition of photosynthesis may be common in clear, shallow wetlands with little light attenuation (Holtgrieve et al. 2010). Light inhibition causes 24-hour oxygen curves to level off at higher concentrations. Standard models, as described above, do not account for light inhibition. Consequently, we used a model by Jassby and Platt (1976) to replace GPP in the standard model with two parameters (P_{max} and α) that cause the rate of GPP to decrease at high irradiances. P_{max} is the maximum rate of photosynthesis before light inhibition slows the rate, and α is the slope of the relationship between GPP and irradiance. We used Akaike Information Criterion to evaluate which of the two models (light saturated or not) provided a better fit for our 24-hour oxygen curves in each season (sensu Christensen et al. 2013).

Seasonal variation

We estimated the total NAP of the pond for each season to test hypothesis 4 by multiplying the average NAP per meter square of each macrophyte by its coverage across the surface of the pond. We used aerial and bankside photography to delineate polygons for each macrophyte type, and we used Google Earth Pro to calculate their areas (Figure 1).

Seasonal changes in ecosystem metabolism may be attributed to an increase in heterotrophic respiration (e.g. sediment and water column bacteria) as temperatures increase over the growing season. Testing this hypothesis required separating rates of autotrophic respiration from rates of heterotrophic respiration in each season. Thus, we positioned four opaque PVC tubes (10 cm diameter) in each treatment patch. One end was gently embedded into the substrate while the other projected above the water line. Two tubes contained the dominant vegetation in each treatment at natural densities, whereas we carefully removed all macrophytes in the two un-vegetated replicates leaving the substrate un-disturbed. This created two treatments: autotrophic respiration + heterotrophic respiration in the tubes containing macrophytes and only heterotrophic respiration in the un-vegetated tubes. At peak oxygen concentrations (~2:00 pm) on Day 2 of both 72-hour periods (spring and summer), we capped all tubes in each treatment patch with aluminum foil to block all light, photosynthesis, and oxygen production. The decline in oxygen concentrations were measured every hour until they dipped below 1.0 mg L^{-1} where the rate of decrease leveled off. If heterotrophic respiration increases

with increasing temperature, then we expected the rate of oxygen decline to be greater in the vegetated tubes in the spring but equally fast between the vegetated and non-vegetated tubes in the summer.

We averaged the replicates and fit smoothed curves of oxygen decrease over time using a radial smoothing procedure (Ruppert et al. 2003) implemented in GLIMMIX in SAS 9.3 (SAS Institute. Cary NC). The fixed effects were presence/absence of vegetation and macrophyte type. We used models in which the curves were exactly the same, they had the same shapes but with different rates to test for the effects of macrophyte type, and where they were different to test for the effect of presence/absence of vegetation on heterotrophic respiration rate during the same season and between seasons for the same macrophyte type. We used a log transformation and Bayesian Information Criterion to select the best fitting model (Schwarz 1978).

RESULTS

Macrophyte Spatial Heterogeneity

Values of GPP and ER were most extreme during the warm summer months (Figure 7) corresponding with the greatest daily variation in the 24-hour oxygen curves. *Chara* patches and green metaphyton patches had the highest average GPP in the spring and summer, respectively (Table 3). On the other hand, green metaphyton patches had the highest ER in the spring and *Chara* patches had the highest ER in the summer. Any GPP recorded in the *Lemna* patches in both the summer and fall was likely attributed to growth of metaphyton and *Chara* because

Lemna is a floating macrophyte so oxygen produced by this macrophyte diffuses directly into the air.

We found significant spatial heterogeneity of net aquatic production among different macrophyte patches (Figure 8a) but not always as we predicted. Contrary to our first hypothesis, NAP was not similar between the two algal patches. Both algal macrophytes made significant or close to significant changes from autotrophy to heterotrophy (*Chara*) and heterotrophy to autotrophy (green metaphyton) from spring to summer (Figure 8a; Table 4). Consequently, green metaphyton patches were significantly more heterotrophic than *Chara* patches in the spring and more autotrophic (but not significantly) than *Chara* patches in the summer. Our results did not support hypothesis 2 as green metaphyton in the spring was also significantly more heterotrophic than *P. foliosus*, whereas the metabolism of *Chara* and *P. foliosus* patches did not differ (Figure 9; Table 4). Thus, the vascular macrophyte was not more heterotrophic than algae as initially predicted. In the summer, we found only partial support for hypothesis 3. That is, heterotrophy was greater in *Lemna* patches than green metaphyton patches as predicted, but it was not significantly different from the other algal treatments (brown metaphyton and *Chara*).

Macrophyte biomass was dropped from this analysis because it was not correlated with NAP. If there was a strong correlation the general pattern in Figure 8a would correspond to the general pattern in Figure 8b. This was not the case as sometimes low biomasses corresponded with high NAP values and sometimes with low NAP values.

Physical and chemical parameters

This pond was not inundated by Hobble Creek in 2013 because the annual snow pack was below average. Consequently, physicochemical parameters were driven by local seasonal weather conditions and not by upstream conditions. Water levels started high in the spring, decreased as evaporation increased in the summer, and increased again in the fall with an increase in rainfall and drop in temperatures. The average (±SE) water volume in our mesocosms followed the same seasonal pattern: spring (146 ± 7.2 L), summer (93 ± 7.7 L), and fall (113 ± 5.2 L). Nutrient levels in this highly eutrophic system also varied seasonally being concentrated in the summer and diluted in the spring and fall (Table 1). Similarly, average daily temperatures also followed a seasonal pattern (Figure 2) reaching a maximum of 37.1 °C in July and a minimum of 7.5 °C in September. However, irradiance was similar among our 72-hour periods and daytime levels only declined during brief periods of cloud cover (Figure 3).

Three oxygen measurements taken in each mesocosm at the same time of day and again at night showed little variation (average coefficient of variation per mesocosm = 0.18) indicating that our sondes provided an accurate estimate of the oxygen concentration within our mesocosms. Average 24-hour oxygen levels in our mesocosms were driven by photosynthesis and respiration, reaching supersaturation during the day and hypoxia at night in the spring and summer (Figure 4 a & b). Oxygen supersaturation occurs when the partial pressure of dissolved oxygen in the water is higher proportionally than the partial pressure of oxygen in the

atmosphere. Thus atmospheric oxygen saturation (100%) occurs when DO matches the atmospheric concentration of oxygen of 20% and a DO supersaturation level of 500% would represent oxygen at 100% of the total gas pressure.

In the fall, oxygen concentrations were determined by the density of *Lemna*. In two mesocosms with the greatest *Lemna* biomass (AFDM = 67.5 g and 38.6 g) all other macrophytes were eliminated by *Lemna* (shading) and were anoxic or nearly anoxic. Two mesocosms with lower densities of *Lemna* contained a mix of *Chara* and metaphyton and, thus, showed dampened diel fluctuations in oxygen. Consequently, there were only brief periods of supersaturation and hypoxia when the four were averaged together (Figure 4 c). Cooler temperatures slowed diffusion which avoided longer periods of anoxia in the fall. Interestingly, the increase in oxygen as irradiance increased was delayed in the spring and fall compared to the summer possibly due to effects of cooler temperatures on rates of photosynthesis. Figure 5 shows that photosynthesis and respiration also produced distinct diel fluctuations of pH and bicarbonate (e.g. Wetzel 2001). This confirms the importance of photosynthesis and respiration, rather than other processes (aeration and atmospheric diffusion), in determining water chemistry and oxygen concentrations in this sheltered pond.

Metabolism calculations

In all cases, the light-saturated model provided the best fit to our diel oxygen curves (see Figure 6 for an example). We used an average piston velocity of 1.93 ± 0.25 m hr^{-1} in the spring,

2.00 ± 0.25 m hr^{-1} in the summer, and 0.93 m hr^{-1} in the fall. Interestingly, the maximum potential photosynthetic rate (P_{max}) of *Chara* was almost twice the value of the other macrophytes in the spring and summer (Table 2). That is, the maximum rate of photosynthesis in *Chara* compared to the other macrophytes indicating that *Chara* was more productive at lower solar radiation. This is noticeable in our summer data when a cloudy day depressed the oxygen concentration in other patches, but not in the *Chara* patch.

Seasonal Variation

This pond produced 551 g O_2 d^{-1} and was autotrophic during the spring. Comparatively, in the summer it produced -533 g O_2 d^{-1} and was heterotrophic, which was consistent with Hypothesis 4. We also predicted that the shift to heterotrophy in the summer would correspond with greater rates of heterotrophic respiration. Our experiment with darkened PVC tubes showed that heterotrophic respiration was slower than autotrophic respiration + heterotrophic respiration in the spring but equal to autotrophic respiration in the summer for both *Chara* and green metaphyton patches (Figure 9). Consequently, compared to the spring, heterotrophic respiration increased in the summer. This may also explain why we found few significant differences in NAP among the macrophyte patches in the summer. That is, differences in vegetation dynamics (photosynthesis versus autotrophic respiration) were overwhelmed by heterotrophic respiration, reducing differences in ER across all treatments because of high rates of heterotrophic respiration.

DISCUSSION

We found that spatial heterogeneity at the scale of individual macrophyte patches determined patterns of ecosystem metabolism in this poorly mixed wetland pond. Specifically, green metaphyton patches were more heterotrophic than both *Chara* and *P. foliosus* patches in the spring, whereas green metaphyton patches were more autotrophic than *Lemna* and *Chara* patches in the summer. We offer two explanations for these differences: one based on potential trait effects on metabolism, while the other suggests the importance of inaccuracies in measuring metabolism in this environment.

First, the response of metaphyton, *Chara*, and *P. foliosus* patches to temperature may explain why metaphyton patches were more heterotrophic in the spring and more autotrophic in the summer than *Chara* and *P. foliosus* patches, which showed the opposite pattern. *Chara* and *P. foliosus* may grow faster than metaphyton in the spring if they are better adapted to cool temperatures as shown in a study of emergence rates in *Potamogeton pectinantus* and *Chara aspera* (Van den Berg et al. 1998). Metaphyton may grow faster than *Chara* and *P. foliosus* as temperatures increase in the summer as warm temperatures (>30 °C) generally favor the growth of metaphyton (Lürling et al. 2013). Light saturation may also play a role by depressing the growth of metaphyton and *P. foliosus* more on cloudy days than *Chara*, which was more tolerant of low irradiances.

In the second explanation, oxygen supersaturation and bubble formation may have caused underestimations of GPP, especially in metaphyton. During photosynthesis oxygen bubbles can form and rise to the surface causing an underestimation of GPP (Odum 1956). In previous studies on ecosystem metabolism in wetlands, oxygen saturation was considered too infrequent to pose a large problem in GPP calculations. For example, the average oxygen concentration in the Everglades was 49% atmospheric saturation, and oxygen was above saturation only 6% of the time (Hagerthey et al. 2010). In our study, oxygen concentration averaged across all treatments and seasons was at 103% saturation, and our oxygen curves were above saturation 41% of the time, with a maximum measured oxygen saturation at 499% (33.47 mg L^{-1}) . We frequently observed bubble formation in the metaphyton patches but never in patches of *Chara* or *P. foliosus*. If bubble formation is more common in metaphyton, then spring estimates of NAP may be less heterotrophic and summer estimates more autotrophic. Thus, differences in NAP between metaphyton and *Chara*, and between metaphyton and *P. foliosus* would be reduced in the spring but increased in the summer. However, metaphyton went autotrophic in the summer when bubble formation was at a maximum. Thus, bubble formation may have reduced the estimate of autotrophy of metaphyton in summer and the estimate of heterotrophy in the spring but it does not appear that such inaccuracies were sufficient to change the general direction of NAP from autotrophy to heterotrophy in the summer. Future research

in similar types of wetlands should account for oxygen saturation by measuring oxygen bubbles released from each patch type.

It is unlikely that there is an aquatic system more influenced by autotrophic processes than this shallow wetland. Our mesocosms and the pond were filled with macrophytes. Yet, heterotrophic bacterial respiration was at least partly responsible for causing a shift to heteroptrophic conditions in the summer. Heterotrophic respiration may have increased in the summer because of higher temperatures and a greater abundance of carbon attributed to decaying *P. foliosus*. This may be a common pattern in shallow wetlands where water temperatures exceed the tolerance of submersed vascular plants.

In this pond, the vegetation patch types varied seasonally with consequences for ecosystem metabolism. Spatial heterogeneity assumes the formation of distinct patches at relevant spatial scales within which processes vary (e.g. Wiens 1995). There was a pattern of clearly delineated patches early in the spring which began to break-down in the summer. Spring patches formed from areas of the pond dominated by specific macrophytes (metaphyton, *Chara, P. foliosus*), whereas in the summer distinct patches decreased as *P. foliosus* declined, metaphyton grew into *Chara*, and *Lemna* began to dominate the macrophyte assembly. By September *Lemna* was the dominant patch type. A previous study has shown that dense growths of *Lemna* can shade and eliminate other macrophytes, often resulting in hypoxic or anoxic conditions (Pokorny and Rejmankova 1987). Dense growths of *Lemna* in our mesocosms also produced

anoxic conditions, but mesocosms with lower densities retained oxygen because of cooler temperature in the fall. Dense growths of *Lemna* in the summer would certainly result in extensive anoxic conditions. Thus, understanding the factors (abiotic and biotic) that drive the rate of succession and can cause a shift between different stable states in these shallow ponds will greatly influence ecosystem metabolism and oxygen availability. To our knowledge, there is little information on the factors that might cause a shift between *Chara* and metaphyton patches versus *Lemna* dominated patches.

Conservation Implications

Riparian ponds can be important habitats for small fish that cannot persist in the stream environment because of intense predation from lotic predators (Archer and Crowl 2014). Also, riparian ponds located near the stream-lake ecotone may be important rearing habitats for potamodromous juvenile fish. Fish that migrate into streams from lakes are often at risk from human activities (e.g. Rader et al. 2010), and riparian ponds may provide warm temperatures, abundant food, and cover from predation for juvenile fish returning to the lake during high flows just as estuaries are important rearing habitat for anadromous species (e.g. salmon) in riverine-marine ecotones (e.g. Ruckelshaus et al. 2002). However, in our study we found that nighttime anoxic conditions were common in every season, but especially during the warm summer months. Consequently, only mosquitofish (*G. affinis*) persisted through the year even though other small fish, including juveniles of endangered species (*Chasmistes liorus*; June suckers), have

been collected in this pond shortly after runoff. Supersaturation of oxygen in water is not generally considered a concern for fish as they are able to adapt to it (Pearson-Le Ruyet et al. 2002). Thus, questions on the factors that determine oxygen concentrations in shallow wetlands are relevant to wildlife managers and specialists tasked with wetland creation. For example, dense growths of vascular submersed macrophytes, *like P. foliosus* should reduce summertime periods of low oxygen if they are capable of persisting through the summer months.

To our knowledge, this was the first study to investigate ecosystem metabolism in a small, sheltered pond at the extreme end of the depth and flow continuum. It was limited to a single pond so future studies should expand to multiple sites in order to increase inference. As is often the case in new explorations, our work has generated as many questions as answers. How does oxygen saturation affect estimates of NAP? Are there general macrophyte traits that may influence metabolism (e.g. vascular tissue, tolerance to high temperatures and light saturation)? What are the factors that drive macrophyte succession and cause a shift between different states? Is there a way to construct shallow wetlands to minimize hypoxia? Future research should address these questions as we seek to maximize the potential of these shallow wetland environments.

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TABLES

Table 1. Average (± one standard error) seasonal nutrient and water chemistry concentrations for all mesocosms in each macrophyte treatment. Spot measurements for Utah Lake and Hobble Creek were provided by The Utah Department of Water Quality.

Treatment	Total N ($mg\ L^{-1}$)	Total P ($mg\ L^{-1}$)	TOC ($mg\ L^{-1}$)	Chloride ($mg\ L^{-1}$)	Sulfate ($mg\ L^{-1}$)	Conductivity ($\mu s\ cm^{-1}$)
Spring						
Chara	2.65 ± 0.04	0.03 ± 0.01	15.03 ± 0.42	30.29 ± 0.15	372 ± 4	1026
Green Metaphyton	2.78 ± 0.06	0.03 ± 0.01	15.93 ± 0.36	31.00 ± 0.08	385 ± 8	1076
P. foliosus	2.7 ± 0.04	0.05 ± 0.01	15.47 ± 0.30	30.33 ± 0.11	365 ± 2	-
Utah Lake June 2014	0.71	0.32	-	163	171	1233
Hobble Creek June 2013	0.95	0.04	-	6	19	327
Summer						
Lemna	5.72 ± 0.32	0.3 ± 0.06	42.83 ± 3.04	49.67 ± 0.36	374 ± 10	1440
Chara	4.15 ± 0.17	0.13 ± 0.02	31.08 ± 2.14	50.48 ± 1.74	478 ± 9	1278
Green Metaphyton	4.35 ± 0.11	0.18 ± 0.02	31.63 ± 1.88	38.95 ± 1.00	410 ± 2	1311
Metaphyton Brown	5.07 ± 0.55	0.14 ± 0.03	34.38 ± 2.44	56.36 ± 0.84	516 ± 7	1523
Utah Lake July 2013	0.95	0.35	-	174	169	1105
Hobble Creek Aug 2013	0.64	0.05	-	4	17	344
Fall						
Lemna	2.59 ± 0.16	0.2 ± 0.03	17.68 ± 0.88	20.07 ± 0.11	286 ± 2	983
Utah Lake Sept 2012	0.74	0.36	-	-	-	1134
Hobble Creek Sept 2012	0.86	0.03	-	19.3	47	542

Table 2. Average values of P_{max} (± one standard error) and α (± one standard error) from the light saturation model.

Treatment	P_{max} (mg O_2 m^{-2} hr^{-1})	α (mg O_2 hr^{-1} W^{-1} m^{-2})
Spring	30.23 ± 2.66	0.08 ± 0.01
Chara	50.34 ± 3.21	0.11 ± 0.02
Metaphyton	25.92 ± 2.41	0.05 ± 0.01
P. foliosus	29.04 ± 6.04	0.09 ± 0.07
Summer	35.40 ± 2.10	0.07 ± 0.01
Chara	49.29 ± 4.99	0.18 ± 0.07
Brown Metaphyton	34.90 ± 2.39	0.09 ± 0.02
Green Metaphyton	35.28 ± 3.90	0.21 ± 0.25
Lemna	21.45 ± 4.56	0.03 ± 0.00
Fall	6.00 ± 1.01	0.25 ± 0.11
Lemna	6.00 ± 1.01	0.25 ± 0.11

Table 3. Seasonal averages (± one standard error) of gross primary production and ecosystem respiration for each macrophyte treatment.

Treatment	GPP ($g\ O_2\ m^{-2}\ d^{-1}$)	ER ($g\ O_2\ m^{-2}\ d^{-1}$)
Spring		
Chara	15.32 ± 0.27	-10.78 ± 0.28
Green Metaphyton	9.83 ± 0.77	-12.43 ± 1.57
P. foliosus	10.20 ± 0.36	-7.70 ± 0.24
Summer		
Chara	11.05 ± 1.11	-13.35 ± 1.80
Green Metaphyton	14.77 ± 0.82	-12.88 ± 0.36
Brown Metaphyton	10.64 ± 1.05	-11.84 ± 0.97
Lemna	7.27 ± 1.14	-10.97 ± 1.29
Summer average		
Fall		
Lemna	3.10 ± 0.44	-3.10 ± 0.16

Table 4. Analysis of variance table showing pair-wise comparisons of net aquatic production (NAP) for each treatment. "ΔNAP" is the difference between the least square means for each comparison.

Comparison	ΔNAP	*t* value	DF	*p*-value
Spring				
Chara vs Green Metaphyton	7.14 ± 1.8	3.8	7.9	**0.005**
Chara vs *P foliosus*	2.04 ± 1.8	1.1	6.0	0.299
Metaphyton vs *P. foliosus*	-5.1 ± 1.8	-2.8	6.0	**0.029**
Summer				
Chara vs *Lemna*	1.72 ± 2.32	0.7	8.4	0.477
Chara vs Brown Metaphyton	-1.20 ± 2.26	-0.5	7.1	0.612
Chara vs Green Metaphyton	-4.19 ± 2.28	-1.8	7.9	**0.103**
Lemna vs Brown Metaphyton	-2.84 ± 2.31	-1.2	7.5	0.257
Lemna vs Green Metaphtyon	-5.91 ± 2.32	-2.6	8.4	**0.033**
Brown Metaphyton vs Green Metaphyton	-2.99 ± 2.26	-1.3	7.1	0.227
Seasonal comparisons				
Chara Spring vs Summer	6.84 ± 2.08	3.3	7.9	**0.011**
Green Metaphyton Spring vs Summer	-4.49 ± 2.08	-2.2	7.9	**0.063**
Lemna Summer vs *Fall*	4.03 ± 0.32	1.7	8.4	**0.118**

FIGURES

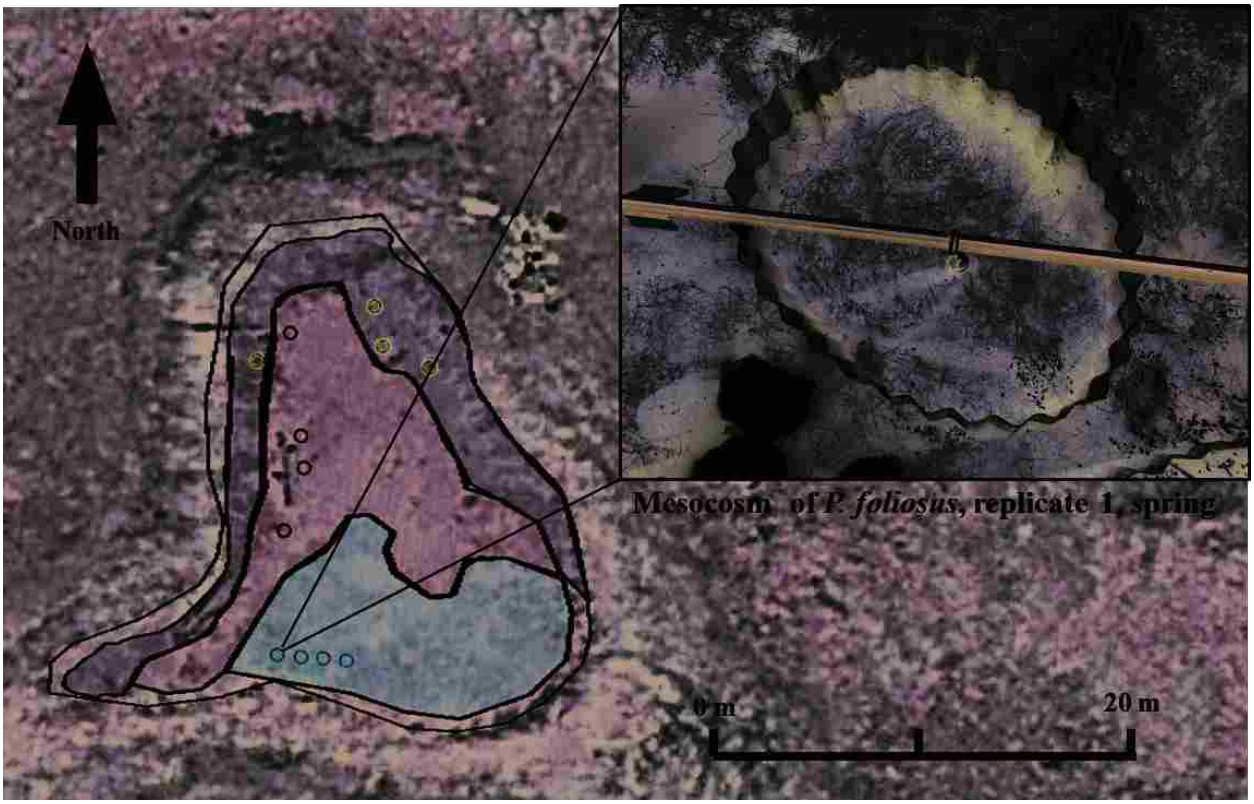

Figure 1. Aerial photograph of the pond showing the relative cover of aquatic macrophytes in the spring: Potomogeton foliosus (red), Chara (green), and green metaphyton patches (yellow). Circles show the location of mesocosms for each treatment. The insert shows a mesocosm and PVC dark-tubes used to measure heterotrophic respiration.

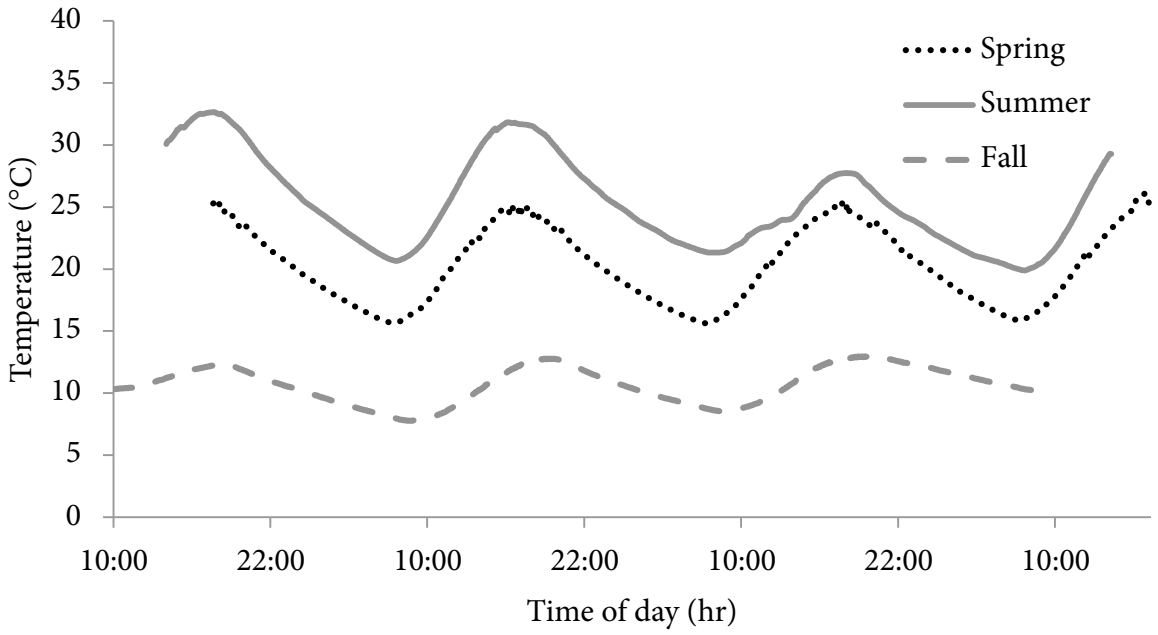

Figure 2. Seasonal average water temperature for each 72-hour period. Data for each period started at different times but each covered 72 hours.

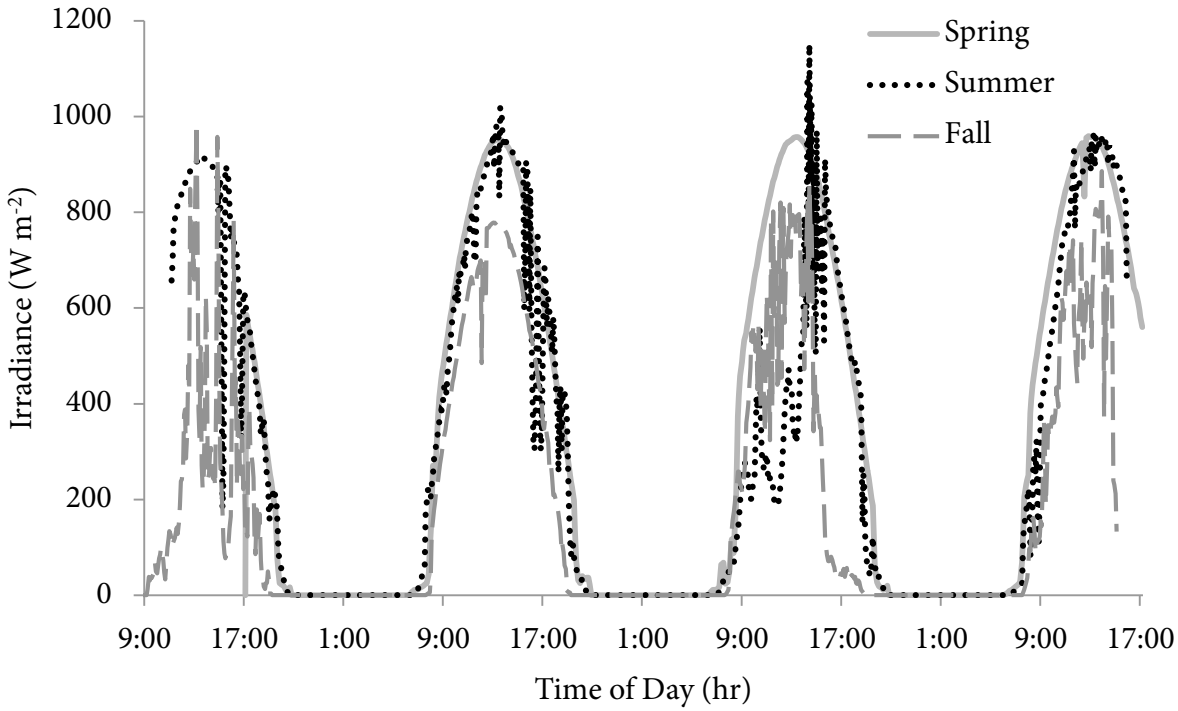

Figure 3. Total solar irradiance (W m^{-2}) for each 72-hour period during the spring, summer, and fall.

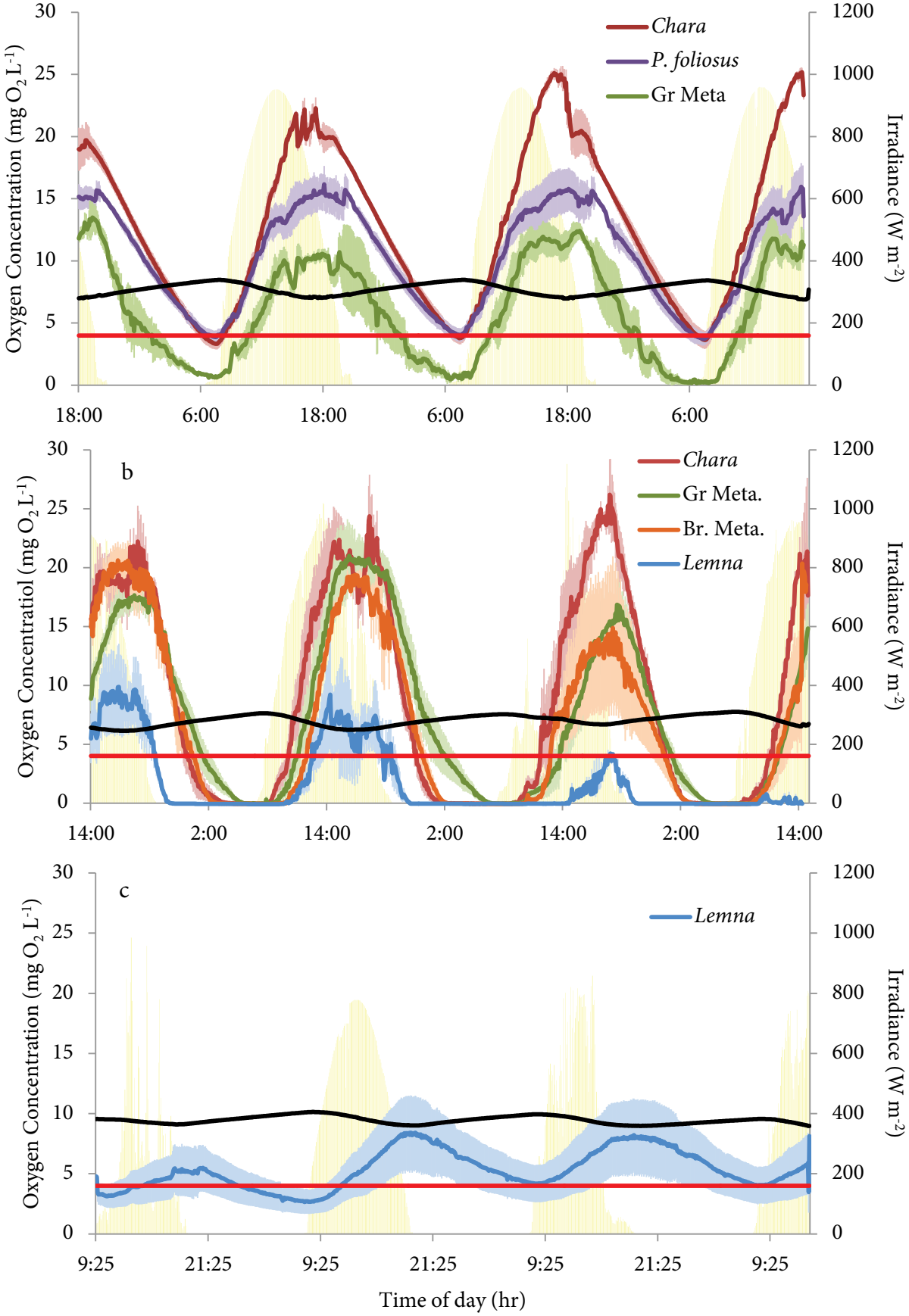
Chara
P. foliosus
Gr Meta
Oxygen Concentration (mg O2 L-1)
Irradiance (W m-2)
18:00
6:00
18:00
6:00
18:00
6:00
b
Chara
Gr Meta.
Br. Meta.
Lemna
Oxygen Concentratiol (mg O2 L-1)
14:00
2:00
14:00
2:00
14:00
2:00
14:00
c
Lemna
Oxygen Concentration (mg O2 L-1)
9:25
21:25
9:25
21:25
9:25
21:25
9:25
Time of day (hr)

Figure 4. Average dissolved oxygen curves for each treatment in the spring (a), summer (b), and fall (c). Shading shows the standard error around each oxygen curve, whereas irradiance is shown as solid yellow curves. Black lines indicate 100% DO saturation, and red lines mark the beginning of hypoxia for sensitive aquatic species. Note that each 72-hour period starts at a different time.

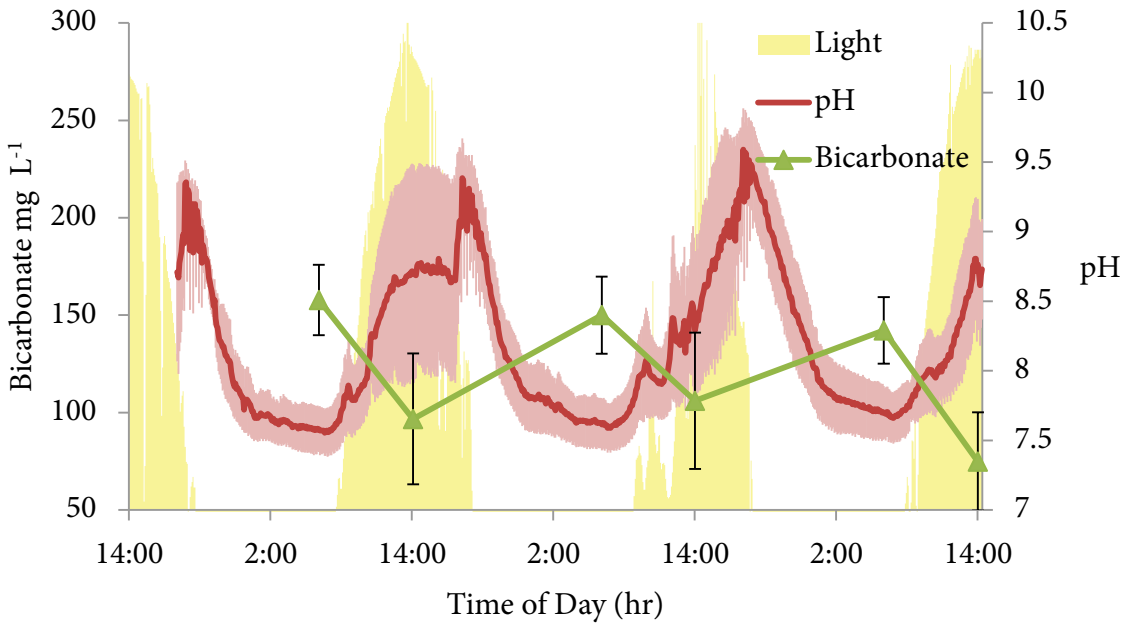

Figure 5. Example of pH and bicarbonate concentrations over a 72-hour period in *Chara* patches during the summer. Shading and vertical bars show the standard errors for pH and bicarbonate (n=2), respectively. Solid yellow curves indicate daylight hours.

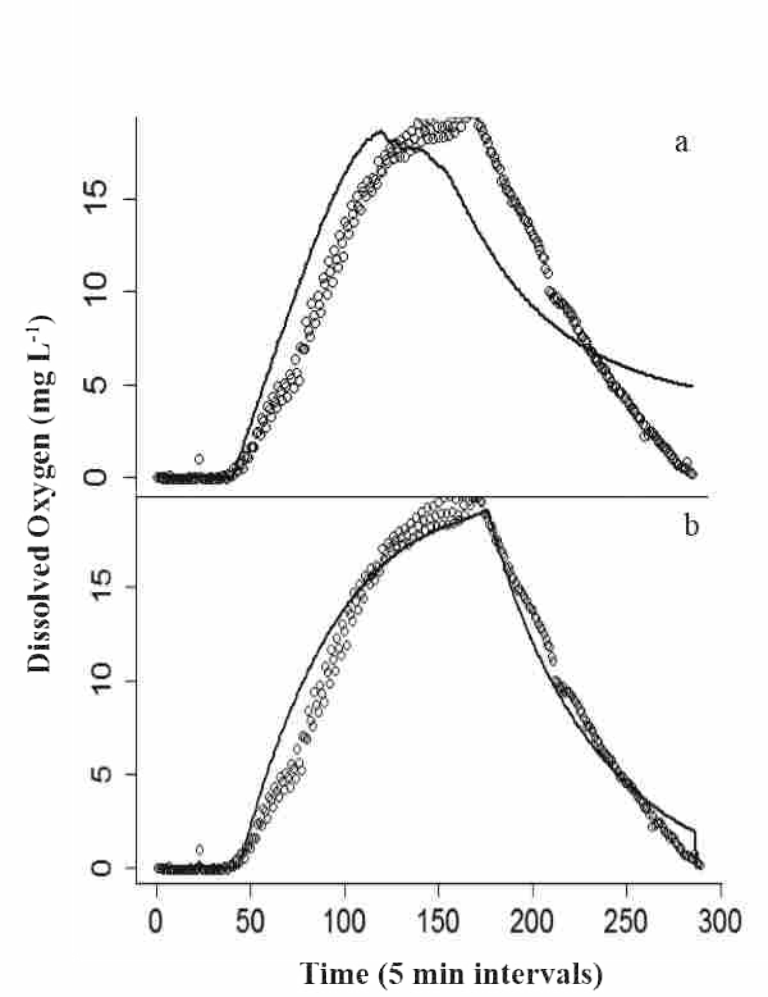

Figure 6. Example comparing the standard metabolism model (a) and a light saturated model (b) fit to a 24-hour oxygen curve for *P. foliosus* patch in the spring. Circles represent oxygen concentration at five minute intervals, and the solid lines show the modelled oxygen concentrations.

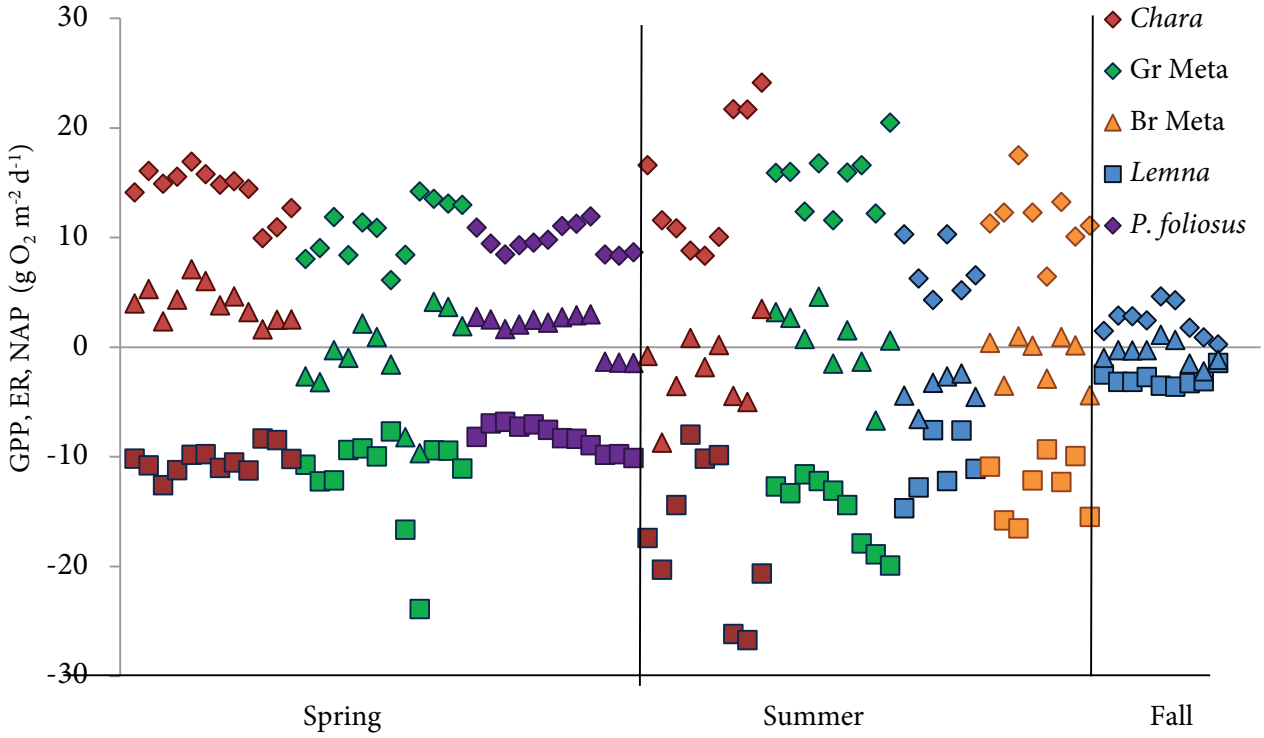

Figure 7. Seasonal plot of gross primary production (diamonds), ecosystem respiration (squares), and net aquatic production (triangles) for each mesocosm in g O_2 m^{-2} d^{-1}.

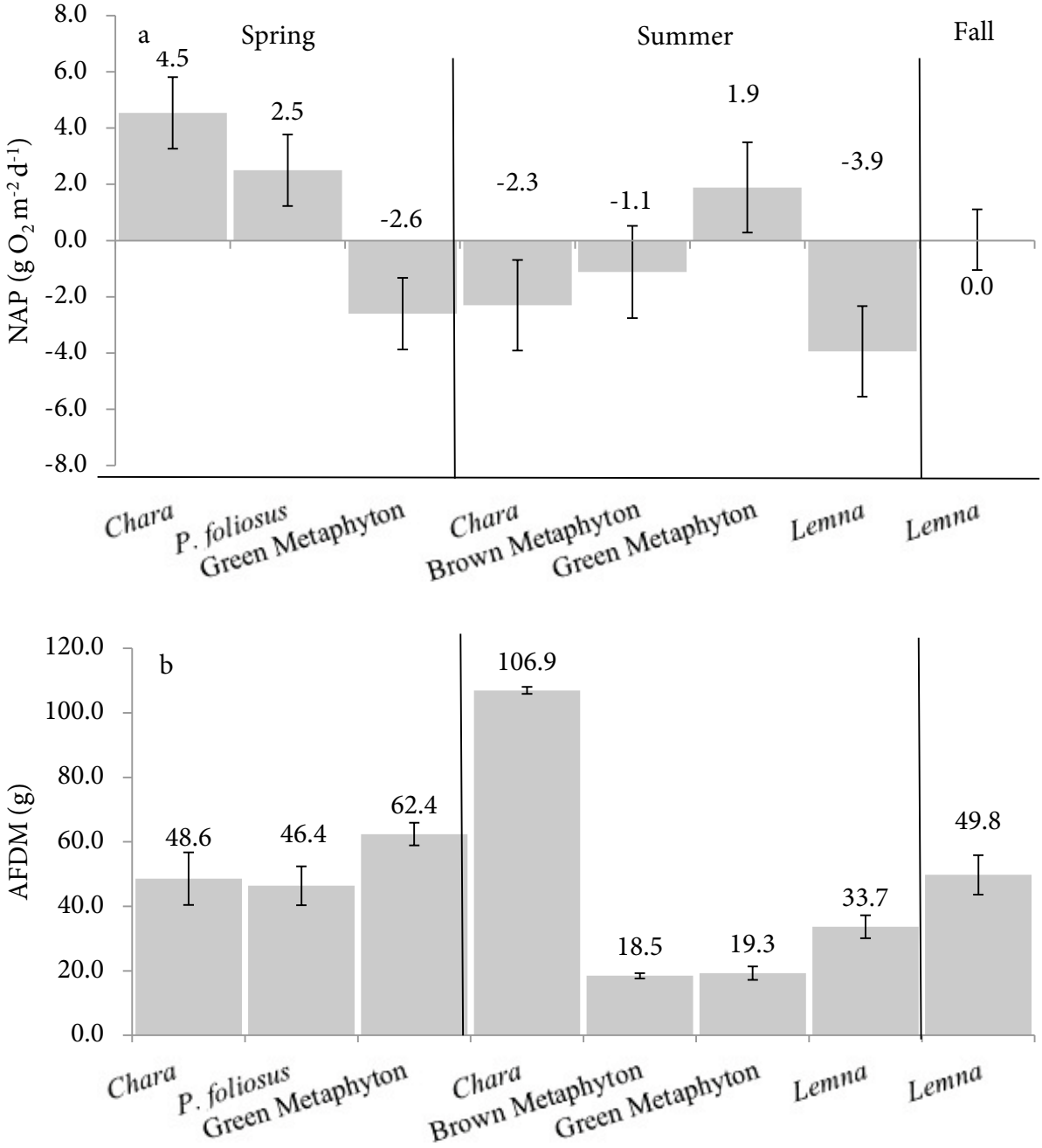

Figure 8. Average net aquatic production by macrophyte treatments across seasons (a). Average ash free dry mass (AFDM) of each treatment (b). Vertical bars represent one standard error around the mean. More replicates would probably have reduced the p-value of nearly significant comparisons.

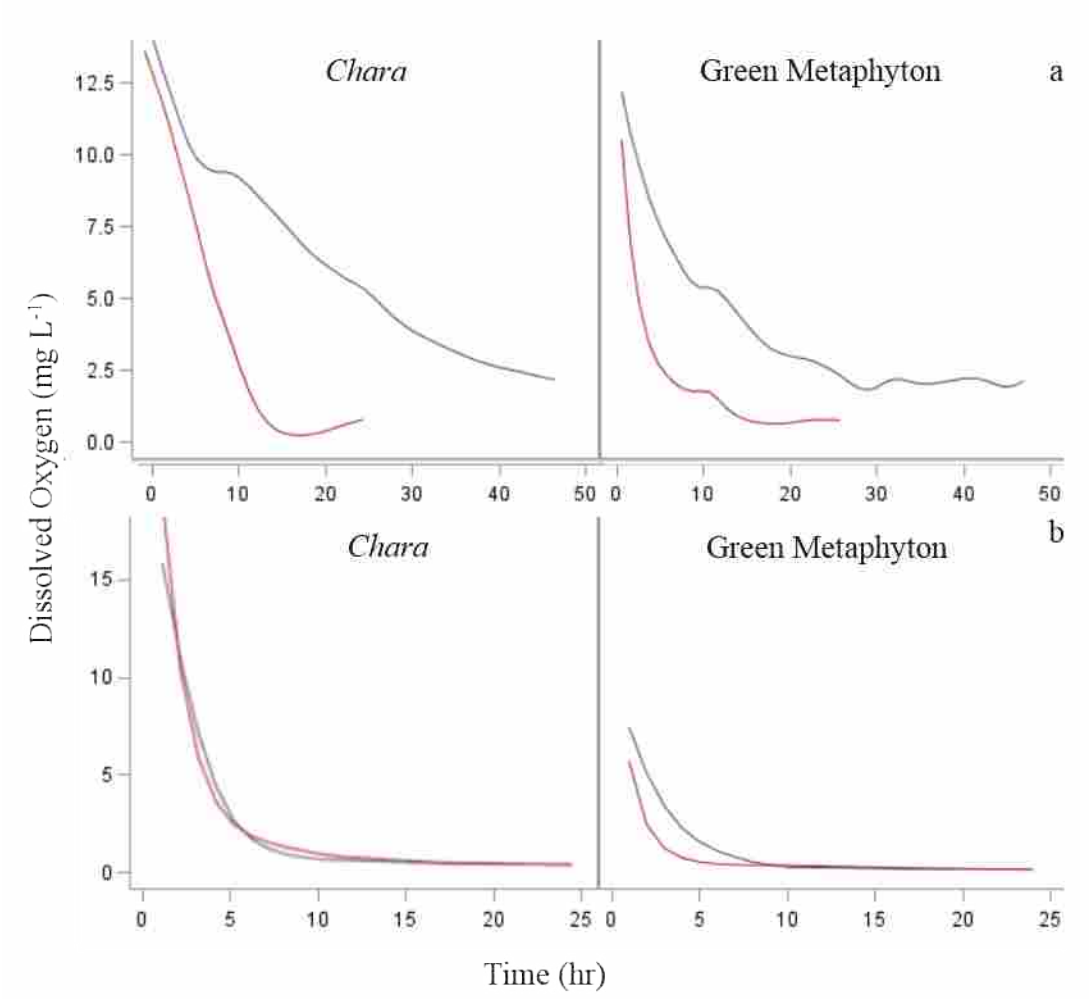

Figure 9. Average rates of autotrophic + heterotrophic respiration (red) and only heterotrophic respiration (blue) in darkened PVC tubes for the spring (a) and summer (b). Chara and green metaphyton were the only treatments occurring in both seasons. Time is hours from when the tube was capped. Note the difference in scale.

APPENDIX

Life and Death in Hobble Creek

D. Riley Rackliffe

Dec 2014

1988 was a good year to be a swamp. That year President Bush enacted a policy that there should be no net loss of wetlands in the United States. He recognized the importance of healthy wetlands in ensuring a clean water supply, habitat for threatened species, and neutralizing toxins. Water is essential to all life, in one form or another and so swamps, perhaps some of the least appreciated landscapes, had their value codified through law. Also, I was born.

But what did it mean? Well, roads must be built, humanity continues to grow, and wetlands frequently make rather nice developments. Essentially the law declared that wetlands could be destroyed when necessary but when they were, new wetlands had to be created to replace them. Suddenly departments of transportation around the nation were giving waterways another look as new roads made them responsible for rebuilding destroyed wetlands. A whole industry of wetland mitigation came alive as lawyers and clerks, engineers and biologists set to work artificially creating what nature had already perfected. Good news for a budding wetland ecologist like me.

In the large flat valleys that I call home the population is centered near two major lakes: Utah Lake and the Great Salt Lake, along with their tributary streams. For years I've watched the

waves of destruction as the city grew to new margins. There is a constant struggle over the shoreline of these lakes as wildlife refuges, environmental groups, highways, and housing developments continue to refine the ownership status of millions of invasive swampy reeds. Not that I'm complaining, as a result millions of dollars are available for research. Without controversy how else could you convince someone to pay you to hang out in a swamp all day?

Three years ago I was hired by a professor to help him study streams in the high Uinta Mountains. My love for those mountains is so profound that I have been guilty of buying a book just because the cover contained a picture of one of my favorite peaks. Spending a summer backpacking obscure mountain lakes seemed like a dream. Well, it was a dream. We spent only seven days in those mountains. The rest of the summer we worked on some government contact to assess a restoration project on a little creek named Hobble just off the freeway a mere 14 minutes from campus.

When most residents in Utah Valley think of Hobble Creek they picture a vibrant Wasatch Canyon with a nice golf course, numerous picnic areas, summer homes, and a few summer camps. This relatively small canyon also produces a perfectly-sized creek which drains the canyon of its annual snowpack. It enters the valley and ends up in Utah Lake, passing through a town called Springville somewhere along the way. As budding biologists we explored those urban stretches of river. Using a well-traveled triangular sweep net we turned over rocks

and dumped whatever insect, worm, or silt happened to float into our net into a Ziploc bag to take back to the lab and process.

Field biology is largely summer work so while it is summer we spend as much time away from the lab as we can. This means our bag of aquatic friends had to stay in one piece until the snows kept us inside long enough to look at them. The easiest way to accomplish this is by dumping a little ethanol; say a 70% solution, over them. They squirm around for a little while but stonefly larvae just aren't designed to survive that treatment. It was hard the first few times, watching the little bugs struggle as the alcohol burned them to death. In my darker moments I wonder if in some heavenly future those 30,000 insects won't come up to me and ask for some sort of explanation as to why I ended their lives prematurely. Dr. Nelson, whose 30 year career in entomology has resulted in the early death of millions of robber flies, assures me that insects are by every measure plenty abundant in this world. After all, this is science, what are a few hundred bugs in the face of scientific exploration? Their deaths will save other insects from the horrific prospect of never existing. This is how wetland scientists work. Without our bags of dead bugs how can we understand the health of the stream?

The abundant water flowing out of the canyon is responsible for the community below it. Hobble Creek allowed for agricultural success in the area although this success relied on getting the water from the creek to the right field at the right time. So the early settlers tamed the stream. It was straightened and dikes built along the banks to prevent flooding and allow more space for

civilization. Dams and diversions were added so irrigation water could share the life of the stream with fields of the valley. As the fields grew larger on the clear clean water of Wasatch snowmelt the lower stream became a drain for all the leftovers. Phosphate and nitrogen fertilizers, motor oil and pesticides, even tires and shopping carts find their way to the concrete channel. The sensitive stoneflies don't live in the lower river.

But even concreted in the backyard of a city a stream is life. Tall trees shade most of the channel which cuts through city blocks regardless of housing, parks, or Main Street. Walking a river is seeing the world from its sewers. Piles of trash, rope swings, a dead muskrat, and overused furniture litter the bottom of the stream channel. Evidence of fishing line and tree forts shows the children have not forgotten the wonder of a stream even if the city has. Just a few yards upstream from the freeway we found a decomposing deer once. Based on the smell it had been there for several days. It must have followed the stream down from the mountains just like we did, staying in the narrow green ribbon of life. Trapped by the city bustle and the freeway it died right there, from what cause I can only guess.

Houses move closer and closer to the stream as the channel became narrower near the center of the city, removing oxbows ponds and backwater pools where young fish used to rest and hide from the larger predatory fish trolling the stream. This part of the stream is home to the trout. I counted 34 of them belly up one sunny July day as we wandered the stream searching for bugs. The creek was flowing, though not much more than a trickle. A man named Joseph who

had his backyard porch swing overlooking the creek at the same spot where we had stationed our thermograph told us the week before the stream had been completely dry. It wasn't a severe drought or a lack of snowpack high in the mountains. Some crops demanded the water so the creek was diverted, down to the last drop. The panicked trout had fled to the few shallow pools left in the deepest parts of the creek. That many fish cannot live long crowded in still water. They breathed in all the oxygen and perished, down to the last fish.

Now, you might think that a few small trout are a small price to pay for agriculture. I'm sure the acres of cabbage or broccoli will feed more people than those trout could. Sure people may notice dead fish, particularly when they are in their backyard. But this isn't the first time Hobble Creek has gone dry, nor will it be the last. Trout will migrate down from the cleaner mountain portion or up from the lake. They will return. They almost always do. Besides, this is industry, what are a few dozen dead fish in the face of feeding humanity?

Another fish however, attracted enough attention that in 1986 it was listed as endangered. The June Sucker is native to Utah Lake and uses the tributary streams like Hobble Creek to spawn. So, using four million dollars of endangered species money and wetland restoration money the last 400 yards of Hobble Creek were fixed and returned to a semi-natural state (along with funding some research experiences for nearby university students). The state purchased a farmer's field and dug up it up to create the sinuous plain that should exist where a river enters a

lake. This small parcel of land, officially a wildlife management area, is exactly what master's projects are made of.

Every few weeks we visit these manmade wetlands to collect one thing or another. We scoop up cups of zooplankton, only knowing they are there by watching them frantically swimming when ethanol is added. Thousands more insects find their way into our plastic bags for later examination in the lab. We beat paths through the restored native plants so we can measure and categorize the vegetation to make sure the proper things are growing there. As it is a popular place for fishermen we frequently run across the abandoned bleached bones of trash fish along the bank. We once brought back a cheek bone for our professor to identify. He identified a carp operculum, snapped it in half, and then went to see if the department chair could ID it.

With seven million pounds of carp in the lake they are a major problem for the June Suckers. Occasionally, if you are quiet enough, you can see the carp swimming through the shallow ponds of our wetland, taking gulps of air since gills can't provide enough oxygen in the shallow warm ponds. The carp don't seem to mind but in the peak of the summer the white bass sometimes go belly up as decomposing algae, fat from the extra phosphates, suck all the oxygen from the water. Low oxygen levels create a perfect home for anaerobic bacteria which takes over decomposition when everything else suffocates. These bacteria give a swamp the characteristic smell and blacken the mud that stains the bottom of our boots.

We spent three days measuring the life-giving oxygen in the water. The first time was in the summer when spending 48 hours camped in a swamp next to the freeway seemed a pleasant adventure. We set up our version of a hobo camp, modeled after the several we had seen along the creek upstream. I brought along a couple books and a knife for wood carving hoping to have plenty of time to enjoy being outside. We had to measure the oxygen every four hours and we soon discovered it took about two hours to complete a round of measurements, leaving a mere two hours between samples for sleep. Standing up to your elbows in a swamp at 3 am makes you question life a little bit. I survived, I'm still a biologist.

We discovered that some logs had blocked the river, raising the water level. This meant that our study sites, disconnected side ponds which serve as June Sucker nurseries, were now all connected in the flowing water. We discussed it with the professor and decided to modify the habitat and restore our system to our preferred natural condition. So we went out and broke down the dam and watched thousands of gallons sweep the channel clean. The next day when we returned with our nets and probes the logjam had been restored completely, with the ponds flooded once more. We decided to let the beavers keep their dam this time.

Three months later we sampled oxygen again. This time the water was warmer than the air. The beavers had continued to alter the ponds so we found the water deeper and with far fewer insects than before, possibly because more stable conditions allowed voracious introduced mosquito fish to spawn unchecked. In one pond we avoided a dead possum on the bank that had

a halo of colored bacteria protecting it. At least the mosquitoes had died in the 40 °F air. The oxygen didn't fluctuate much in the fall. The algae had mostly died out and colder temperatures slowed the decaying processes.

I returned to those ponds again the next summer. Instead of the 100 or so oxygen measurements we scaled up to 80,000 measurements. That's enough for a master's thesis. It turns out that each kind of plant has its own part to play in the system. Even focusing on the underwater plants in a single pond there is a complex battle over space being waged. The alga species fight with the vascular plants until the floating plants come in and shade everyone else into a darkness that means death to photosynthesizers. In the July heat of this battle the vegetation is so intense that photosynthetic oxygen drives all the nitrogen out of the water, resulting in oxygen supersaturation. At least until sunset when oxygen plummets within 45 minutes and remains at zero throughout the night. It's enough to reduce whatever metal my ring is made of turning the silvery color into a burnished bronze.

A year later the equipment is all in. Research concluded, for now. There are a few trails left in the cattails and planks of wood which we decided were equivalent to decomposing trees. The creek flows on, no longer obstructed by the beavers that had disappeared unexpectedly the previous spring. There is a fence post hidden under a cottonwood tree that I will go and collect any day now. Maybe when I go and say goodbye.

Wetlands are complicated places. They are the drains of the world, ignored until they fail. They collect the salts, phosphates, decomposing leaves, and lost plankton of whatever lies upstream into warm shallow pools for processing before releasing them into the lake. Pools of rotting ooze feed billows of midges and mosquitoes. The swarms of flies feed the flopping carp and dithering white bass, keeping them fed until the juvenile June Suckers or black bullhead catfish appear to give them larger snacks. All the dead and dying from Hobble Creek and Springville wash down to this place where the bacteria, with or without oxygen, will perform the thankless job of breaking them down to feed the next generation. Cottonwoods and willows, cattails and bulrushes, pondweed and algae suck up the nutrient rich water in yearly bursts of productivity. Ducks, herons, ibis, and pelicans take their turn as fox, raccoon, beaver, feral cats, and water rats nibble at the margins: all thriving life hanging on at the end of the line.