SPATIOTEMPORAL DYNAMICS OF HYPOXIA IN DENSE HYDRILLA WITH IMPLICATIONS FOR FISH HABITAT QUALITY

By

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To my family and friends

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DO	Dissolved oxygen
FDEP	Florida Department of Environmental Protection
GPS	Global Position System
KGM^{-2}	Kilograms per meter squared
MGL^{-1}	Milligrams per liter
USDA	United States Department of Agriculture

Abstract of Thesis Presented to the Graduate School
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The fast, dense growth and architecture of some macrophyte species can alter water chemistry and impact fish habitat quality and quantity. Hydrilla *Hydrilla verticillata* is an invasive aquatic weed which exhibits rapid growth and may contribute to low dissolved oxygen concentrations (hypoxia, DO <2.0 mgl^{-1}) during warm summer months. I evaluated the spatial and temporal dynamics of dissolved oxygen in three habitat types: open water, edge of hydrilla beds, and the dense hydrilla bed interior at two Florida lakes. My results showed that habitat type, month, and depth all significantly influenced dissolved oxygen, and up to 100% of the water column was hypoxic in late summer in the small lake. However, consistent, high biomass density coupled with peak temperature earlier in the season did not produce hypoxic conditions, suggesting that other factors are influencing dissolved oxygen in this habitat. Complete water column hypoxia was not seen and hydrilla density was much less in the larger lake. Lake morphology and size may influence the density and impacts of hydrilla on water quality. Additionally, hypoxia in edge habitat indicates that increasing ecotone may not greatly influence DO concentrations unless substantial open water area

adjacent to dense beds is maintained for adequate water cycling. However, maintaining edge habitat is beneficial by increasing macroinvertebrate communities and predatory efficiency, and for navigation by recreational boaters; thus, managers should consider this method in an aquatic weed control program.

CHAPTER 1
INTRODUCTION AND BACKGROUND

There are an estimated 25,000 nonindigenous plants in the United States, with an approximate total cost of $110 million in damages and control for aquatic weeds (Pimentel et al., 2005). Noxious aquatic weeds such as Eurasian watermilfoil (*Myriophyllum spicatum* L.), waterhyacinth (*Eichhornia crassipes* (Mart.) Solms), and hydrilla (*Hydrilla verticillata* L. f.) were likely introduced from warmer areas of Asia as ornamental species and spread intentionally or accidentally (Langeland, 1996; Kay & Hoyle, 2001). These species are now invasive across the United States (USDA, 2011) due to phenotypic plasticity, genetic variability, and adaptation ability (Theoharides & Dukes, 2007). Advantageous morphology, rapid growth, and several modes of reproduction allow aquatic weeds to establish in new habitat and often alter ecosystem processes (Gurevitch et al., 2006; Hershner & Havens, 2008).

Aquatic systems are some of the most anthropogenically impacted ecosystems in the world due to altered hydrology via flood control and hydropower projects, as well as invasive species introductions. The cost and difficulty of eradication projects for invasive species has led some ecologists to consider whether various invasive species offer beneficial ecosystem services, rather than managing in attempt to restore the system to a condition found prior to invasion (Hershner & Havens, 2008). Total restoration of systems with aquatic weeds is rarely feasible, and thus consistent, practical, and affordable management may be a more sustainable goal.

Hydrilla verticillata

Hydrilla *Hydrilla verticillata* is an invasive aquatic weed first discovered in Florida in 1960 and has since spread across the United States (Langeland, 1996; USDA, 2011). Four possible modes of reproduction (fragmentation, tubers, turions, and seed) allow it to spread quickly and easily, particularly through fragmentation (Langeland, 1996). Furthermore, it is difficult or impossible to eradicate hydrilla after tubers are produced in the soil due to persistent re-infestation (Haller & Sutton, 1975). Tangling and breaking on boat propellers, boat trailers, and waterfowl heightens propagule pressure and greatly increases likelihood of establishment (Theoharides & Dukes, 2007; Richardson, 2008).

Hydrilla grows vertically by stems and horizontally by rhizomes and extensive branching. Expansion of primary and lateral shoots can result in rapid accumulation of biomass (Glomski & Netherland, 2012). Dense branching by stems as they reach the water surface creates a thick mat, so that 50-80% of the standing crop of hydrilla occurs in the upper 0.5 m of the water column during summer when biomass is at a maximum (Haller & Sutton, 1975). The dense mat can span the entire water column in shallow areas and water bodies (Hoyer et al., 2005), which are particularly common in Florida. The dense surface mat decreases light transmission to below the saturation point necessary for many submersed aquatic vegetation (SAV) species (Bowes et al., 1979). Hydrilla, however, has low light requirements which allow it to sometimes continue growth beneath its canopy and in deeper water than is possible by many submersed macrophytes (Bowes et al., 1977; Langeland, 1996).

While many studies suggest a loss of aquatic plant diversity with the invasion of hydrilla (Gordon, 1998; Colle & Shireman, 1980), few have tested this empirically. A community study by Hoyer et al. (2008) compared Florida lakes with and without hydrilla infestations, found that occurrence of hydrilla did not cause reductions in species richness for aquatic plants, aquatic birds, or fish in lakes. Regardless of community impact, the density and rapidity of hydrilla growth necessitates management and control for navigation, flood control, and recreational use on lakes and rivers (Madsen, 2009).

Aquatic Plants as Fish Habitat

Aquatic plants function as important fish habitat. Plant beds serve as a nursery for young and small fish, offering foraging ground and cover from predators (Rozas & Odum, 1988). Vegetated habitats support higher abundance and diversity of fish than do unvegetated habitats, and fish density is positively correlated with abundance of macrophytes (Barnett & Schneider, 1974; Diehl, 1988; Rozas & Odum, 1988; Miranda & Hodges, 2000). Higher complexity may also reduce aggressiveness and allow for higher numbers of territorial species if habitat is broken up (Basquill & Grant, 1998; Höjesjö et al., 2004). Due to higher surface area for attachment (stems and leaves), increased vegetation complexity also promotes higher macroinvertebrate density and diversity, which are important food resources for juvenile largemouth bass (*Micropterus salmoides*) and sunfishes (*Lepomis* spp.; Crowder & Cooper, 1982; Tate et al., 2003).

However, there is dispute as to how much cover/density is beneficial for fish populations. Some authors argue that excessive cover (>50%) and density decreases foraging and predation efficiency (Crowder & Cooper, 1982; Savino & Stein, 1982). This may cause some predatory species to change their behavior from active searching to ambush strategies (Savino & Stein, 1989) and a reduced growth rate in prey fish (Colle & Shireman, 1980). Conversely, higher encounter rates due to increased populations of prey species may compensate for lower predator efficiency (Savino & Stein, 1989). Thus there is debate as to whether high density macrophytes reduce growth rate of fishes (Savino et al., 1992).

High-density macrophyte growth can dramatically alter the chemical environment, impact native species survival and adaptation, and ultimately transform ecosystem communities (Gordon, 1998; Carroll, 2007). The reduction in dissolved oxygen due to dense macrophyte respiration can render this habitat unsuitable for many fish species (Bowes et al., 1979; Caraco et al., 2006; Bunch et al., 2010). Kaller et al. (2011) and Caraco et al. (2006) found the morphology of vascular aquatic plants (i.e. complexity, growth form) to significantly influence dissolved oxygen concentrations. Similar to terrestrial plants, aquatic plants perform carbon fixation via photosynthesis during the day and respiration at night, causing a depletion of DO during night and early morning hours (Zelitch, 1975). Moreover, dense surface canopies reduce water circulation and sunlight transmission through the water column, limiting photosynthesis beneath the canopy (Bowes et al., 1979). As water temperatures rise over the summer season, oxygen solubility decreases (Powers, 1980; Kaller et al., 2011). The compounding effects of macrophyte growth, diel flux of photosynthesis and respiration, and warm temperatures may result in periods of hypoxic conditions (DO <2.0 mgl-1; Bowes et al., 1979; Caraco et al., 2006; Bunch et al., 2010).

Hypotheses

I hypothesized that 1) hydrilla causes dissolved oxygen concentrations to decrease to hypoxic levels which can extend throughout the water column at night. Furthermore, I hypothesized that 2) given the heterogeneous growth of vegetation, microhabitats of elevated DO concentration exist in dense beds and can act as points of refuge allowing fish to remain in hydrilla habitat. Finally, I hypothesized that 3) the edge of dense beds (i.e., the open water-dense hydrilla interface) exhibits improved dissolved oxygen concentrations, with potential for managing hydrilla to maximize edge habitat and improve dissolved oxygen. In this paper, I present the results of my study investigating spatiotemporal dissolved oxygen dynamics in dense hydrilla in two Florida lakes to evaluate the quality of hydrilla as fish habitat.

CHAPTER 2
SPATIAL AND TEMPORAL DISSOLVED OXYGEN DYNAMICS IN DENSE HYDRILLA IN TWO FLORIDA LAKES

Introduction

Submersed macrophytes offer beneficial fish habitat by providing ample food resources and refuge from predators (Crowder & Cooper, 1982). However, macrophytes at high densities can impact water quality (Caraco et al., 2006). Invasive aquatic plants frequently obtain higher biomass and coverage than many native plants due to rapid growth, lack of natural predators, and adaptation ability (Gurevitch et al., 2006). The morphology of macrophyte species, such as submersed branching and leafing or floating-leaved forms, can contribute to low dissolved oxygen by shading sunlight during the day, increasing respiration at night, and reducing water circulation (Bowes et al., 1979; Caraco et al., 2006).

Hydrilla *Hydrilla verticillata* is an invasive aquatic weed exhibiting dense shoot production throughout the water column with a thick, branching mat at the surface. This species supports high abundance of small and young fishes attracted by structural habitat and macroinvertebrate resources (Barnett & Schneider, 1974; Tate et al., 2003). However, an inverse relationship between vegetation density and dissolved oxygen may influence how fish use this habitat (Miranda & Hodges, 2000; Burleson et al., 2001). High biomass with overnight respiration combined with warm water temperatures during summer can potentially result in hypoxic (DO <2.0 mgl^{-1}) conditions considered unsuitable by some popular sport fishes such as largemouth bass and bluegill sunfish (Moss & Scott, 1961; Miranda et al., 2000).

During periods of hypoxia, fish may remain in the hydrilla habitat by finding microrefuges of higher DO within the dense stand, similar to those observed by Miranda et al. (2000) in dense southern naiad *Najas guadalupensis* beds. Conversely, fish may migrate to other habitat types (e.g., open water) with improved dissolved oxygen concentrations (Suthers & Gee, 1986). However, moving to these alternative areas may increase risk by predatory species and thus reduce survival rates of juvenile fish if hypoxia and migration is a frequent occurrence (Savino & Stein, 1989).

Studies investigating fish-plant interactions are often conducted on broad, “macroscales” of whole water bodies or water body zones, and fewer studies have evaluated aquatic plant habitat on a “microscale” more relevant to individual or groups of fishes (Dibble et al., 1996b). Dissolved oxygen readings are often collected at only a few points or by autonomous data loggers, and seldom explore the heterogeneity of habitat types on a finer spatial scale (Carter et al., 1991; Miranda & Hodges, 2000; Caraco & Cole, 2002; Rose & Crumpton, 2006). Broader studies may generalize relationship between aquatic plant abundance and potential fish habitat use. Dibble et al. (1996b) suggested that systems should be investigated at smaller scales relative to structural and functional habitat conditions that are directly relevant to fish habitat use and behavior. In this study, I evaluated dissolved oxygen at a spatial and temporal “microscale” (over a scale of meters horizontally and vertically, and over hours of a day) which then allowed us to make broader implications for large-area applications and season. My objectives were to 1) assess the occurrence of hypoxia throughout the water column (“complete” hypoxia) in dense hydrilla, 2) explore the existence of microrefugia within hydrilla beds, 3) examine the spatial extent of hypoxia across three habitat types (dense hydrilla bed interior, edge of dense beds, and open water), and 4) compare dynamics between two lakes.

Methods

Study Areas

Sampling took place on Sandmine Lake (28°91 N, 81°57 W) (Figure 2-1) in Lake County and Lake Tohopekaliga (28°10 N, 81°23 W) (Figure 2-2) in Osceola County, Florida. Sandmine Lake is a 97-hectare man-made lake and former sandmine operation in the Lake Norris Conservation Area, owned by the St. Johns River Water Management District (SJRWMD, 2011). It is located in a geological region characterized by the Miocene Formation, Hawthorne Formation, with sand, silt, and clay (UF IFAS, no date) soil composition and a depth range of 2-9 meters. The study area was primarily located in the southern end, adjoining to the deepest portion (mining area) of the lake where consistent open water was found with adjacent dense hydrilla beds. The hydrilla bed sampled was approximately 1.5 acres in size. The overall hydrilla coverage of the lake reached over 90% by late summer (Figure 2-1). Dense habitat sampling locations were an average 24.8 m from the edge of the dense bed, and an average 55.0 m from sampled open water sites (Table 2-1).

Lake Tohopekaliga is a 9,800-hectare lake in the Kissimmee Chain of Lakes, and a popular sport fishing destination in central Florida. The geological region is characterized by the Plio-Pleistocene formation, Jackson Bluff Formation, with silty, shelly sand (UF IFAS, no date) sediment and a depth range of 2-5 meters. The study area was located in Goblet’s Cove, a 430-ha bay on the eastern portion of the lake. By September, 60% of Goblet’s Cove contained surface-matted hydrilla (Figure 2-2). Dense habitat sampling sites were an average 148.8 m from open water sites and 68.5 m from edge habitat sampling sites (Table 2-1). Lake Tohopekaliga is heavily managed for its sport fishery, recreational boating, and the endangered snail kite (*Rostrhamus* *sociabilis*). Both lakes contain fish species common to Florida, including sportfish such as sunfish, largemouth bass, and black crappie (*Pomoxis nigromaculatus*).

Dissolved Oxygen Sampling

I used Yellow Spring Instruments (handheld YSIs, Model 556 MPS and Model 85; stationary YSIs, Model 600 OMS) multiparameter sondes and Hach Environmental (stationary Hydrolabs, Model MS5) optical water quality sondes to evaluate the spatial and temporal fluctuation of dissolved oxygen (mgl^{-1}) during summers 2011 and 2012. In 2011, I conducted a pilot study to verify the occurrence of hypoxia throughout the water column ("complete" hypoxia) in dense hydrilla beds. I set stationary YSIs and Hydrolabs to record DO concentrations every 30 minutes for 2 days, monthly from March – May 2011 for preliminary dissolved oxygen sampling in dense hydrilla from. Data was then collected monthly with handheld YSIs from June – September to assess the spatial and temporal extent of hypoxia in this habitat type over the summer season. Handheld sampling was during early morning hours when DO was expected to be lowest due to nightly macrophyte respiration (Hannan & Anderson, 1971); specifically, this ranged from three hours before dawn until a maximum of four hours after dawn. Random locales within dense hydrilla beds consisting of four to six samples were taken at least one meter apart for a total of 25 samples and marked with Global Positioning System (GPS) receivers (Garmin GPSMAP 76CSx). Each locale was a minimum one boat length from the previous location. Samples were taken at three depths: surface (0.00-0.61 m), mid (0.61-1.21 m), and deep (1.21-1.82 m). In September 2011, handheld sampling was extended to five days and sample sizes increased in order to detect evidence of elevated oxygenated microhabitats within the dense hydrilla bed. I also set the stationary sondes to record DO concentrations every 15 minutes for 10 days in 3 habitat types (dense hydrilla bed interior, edge of hydrilla bed, and open water) at the surface (0.00-0.61 m) and mid (0.61-1.21 m) strata.

To capture higher spatial resolution in 2012, I expanded handheld sampling to again to include the dense hydrilla bed interior, as well as edge of hydrilla beds and open water. Both Sandmine Lake and Lake Tohopekaliga were sampled. I also performed afternoon sampling to determine the duration and spatial extent of hypoxic conditions. Afternoon sampling was conducted when maximum DO concentrations were reached; specifically, from four hours before dusk until a maximum of one half hour after dusk. Four random locales within each habitat type (dense, edge, and open water) consisting of six to seven samples each were taken at least one meter apart for a total of 25 samples and marked with GPS receivers (Garmin GPSMAP 76CSx). Samples were taken at three defined depths: surface (0.00-0.61 m), mid (0.61-1.21 m), and deep (1.21-1.82 m) for both, early morning and afternoon sampling at both lakes, monthly from June – October. I did not use stationary sondes for the 2012 season.

Although the lake bottom was occasionally deeper than 1.82 m in both lakes, the Florida Department of Environmental Protection (FDEP) recommends DO sampling be conducted in the upper half of the water column, or upper two meters where lakes exceed a total depth greater than four meters (FDEP, 2012). This is because this zone is most often utilized by the fish and invertebrates under consideration (FDEP, 2012). Therefore, my results describe this portion of the water column.

The “dense” habitat type was visually determined by surface-matting, and samples taken at least several meters from any open water area (Figure 2-3, Table 2-1). “Open water” was where rippling or wave action was evident and no vegetation was seen. Occasionally, sparse vegetation was collected on the anchor in open water indicating limited macrophyte growth on the bottom, but was not in significant amounts and thus I maintained this area as “open water.” “Edge” habitat types varied between lakes due to differing depth changes. Sandmine Lake, as a man-made lake, has very sudden depth changes which results in a well-defined edge line (Figure 2-4). Dissolved oxygen samples were consistently recorded on or within 2 m of the well-defined interface. Lake Tohopekaliga has very gradual depth changes which results in a progressive transition between dense hydrilla and open water; “edge” locations were selected visually as a location with sparse hydrilla stemming, without surface-matting.

Currently, the minimum dissolved oxygen standard is set at 5.0 mgl^{-1} by the FDEP (2012). However, a statewide review of Florida lakes and rivers revealed that 52-70% fail this criterion (FDEP, 2012). The state of Florida has now proposed a new DO criterion based on regional regression analysis of average condition indices and daily average DO saturation to determine minimum DO concentrations for systems experiencing naturally-low DO. This analysis concluded that DO saturation of 38% reached during the daily workday period (8:00 – 17:00) is necessary for healthy biological systems in Peninsular Florida (FDEP, 2012). Water temperature in late summer (September) during 2011 reached 27.97°C, equating to 3.0 mgl^{-1} DO for 38% saturation. Previous studies suggest the hypoxia tolerance of centrarchids is limiting when DO drops below 1.0 mgl^{-1} for extended periods of time, usually resulting in mortality (Moss & Scott, 1961; Miranda et al., 2000). With consideration of this report, the typical diel cycle of oxygen output and uptake by plants, and primary literature on the hypoxia tolerance of fishes, I categorized dissolved oxygen concentrations and hypoxia as “severe” being less than 1.0 mgl^{-1}, “stressful” being 1.0-2.0 mgl^{-1}, and “adequate” being over 2.0 mgl^{-1} (Moss & Scott, 1961; Miranda et al., 2000).

Vegetation sampling

I also collected hydrilla biomass samples to compare relative vegetation density with dissolved oxygen concentrations in the two lakes. A vertical biomass rake (Johnson & Newman, 2011; Figure 2-5) was used to collect hydrilla samples at four random locations within dense hydrilla beds. Samples were taken at Sandmine Lake monthly, from March 2011 – October 2012. Biomass samples were taken monthly during summer 2012 at Lake Tohopekaliga. When handheld sampling was conducted, vegetation was collected in the same dense hydrilla bed that was sampled for dissolved oxygen. The rake was lowered to the bottom, rotated three times, and raised to the surface. Vegetation was returned to the lab and placed in a dry oven set at 77-79°C for a minimum of 48 hours, and weighed. Biomass was estimated by the sediment area sampled by the vertical rake with four, 7.62-cm tines, which equates to a 0.02-m^2 area. Samples were averaged and extrapolated to kgm^{-2} dry weight.

Analysis

To obtain descriptive statistics from September 2011 time series data collected by the remote stationary sondes, I systematically extracted dissolved oxygen concentrations every 2 hours during the night/early morning periods, which I considered from four hours after dusk to four hours after sunrise to account for DO minimums and maximums. This allowed me to obtain an adequate sample size (n=60) per habitat and depth. I used mixed effects analysis of variance (ANOVA) model to determine if DO varied by habitat type (3 types: dense, edge, and open water) or depth (2 depths:

surface and mid) in full factorial design with hour as a block factor (6 hourly recordings) and day (10 days) as a random effect (DO~Habitat*Depth+Hour+Error(Day)).

For 2012 handheld data, analysis of variance (ANOVA) was used to determine if dissolved oxygen varied by month (4 or 5 months: June – September/October), habitat type (3 types: dense, edge, open water), and depth (3 depths: surface, mid, deep) in full factorial design, with lake as a block factor (DO~Month*Habitat*Depth+Lake) for the early morning time period. Factorial design was chosen a priori because I believed that all factors could influence dissolved oxygen simultaneously. The analysis considered only the early morning time period because this was shown as the only possibility for widespread hypoxia based on the 2011 pilot sampling data.

I determined the percentage of hypoxic habitat by calculating the sum of the each depth (surface, mid, deep) that was hypoxic in each habitat type, divided by the total sampling depth (1.82 m). I could then estimate the percent of unsuitable habitat due to hypoxia temporally by month and spatially by habitat type and depth, in this zone.

Results

Dissolved Oxygen Sampling

Sandmine Lake

The dense hydrilla canopy was at or near the surface at the beginning of the sampling season in March 2011. Preliminary dissolved oxygen sampling showed DO was well above the threshold of hypoxia (Figure 2-6). Consistent hypoxia was seen in the deep stratum by April, and by May mid-level of the water column experienced a diel fluctuation of hypoxic conditions. Although we saw hypoxia extending through the mid-stratum as early as May, we did not detect complete hypoxia (hypoxia extending the entire water column) until September in dense hydrilla (Figure 2-7). While hydrilla beds became hypoxic during early morning hours in September, hypoxia severity was variable by location at the surface level (Figure 2-8). Thus, some areas contained DO values between 1.0-2.0 even though much of the area was severely hypoxic throughout the water column in September.

The mixed effects ANOVA model of stationary sonde DO extractions in September 2011 showed all main effects to be highly significant (ANOVA, $P<0.0001$) in influencing dissolved oxygen. However, the interaction was not significant (ANOVA, $P=0.304$). Tukey's Honestly Significant Difference test was used for post-hoc analyses to evaluate differences in habitat type. Open water habitat type showed to have significantly higher DO than either dense or edge habitat types (Tukey HSD, $P<0.0001$), however edge did not have significantly higher DO than dense habitat type (Tukey HSD, $P=0.794$). Time series data showed a diel cycle of dissolved oxygen in all habitat types, with greatest fluctuations occurring in the surface strata (Figure 2-9). Dense and edge habitat types had the highest occurrence of hypoxia. Conversely, open water rarely declined below 2.0 mgl^{-1}, even in the mid-stratum. Time series DO extractions result in a night/early morning average, versus the early morning minimum obtained through handheld sampling; this is likely the reason Hour was found to be a significant factor in the mixed-effects model. Therefore, although handheld sampling showed hypoxia extended throughout the water column in dense habitat, descriptive statistics of time series data showed DO concentrations to be at or above the threshold of hypoxia for all habitat types at the surface level (Table 2-2).

In October 2012, hurricane Sandy caused inclement weather conditions for the monthly sampling trip. Consequently, only 15 samples were obtained for each habitat type and depth at Sandmine Lake for early morning sampling, and no afternoon dissolved oxygen sampling was possible. Dissolved oxygen data and vegetation collection was also unattainable at Lake Tohopekaliga for October 2012.

For early morning data in 2012, the ANOVA model showed all main effects (month, habitat type, and depth) and lower-level interactions were significant (ANOVA, $P<0.05$) (Table 2-3). However, the three-way interaction was also significant, indicating that all factors in combination had substantial influence over dissolved oxygen during the summer season (ANOVA, $P<0.01$). Lake as a block factor was also highly significant (ANOVA, $P<0.0001$), suggesting that accounting for lake effects in DO explained significant variance in the factorial ANOVA.

Tukey's Honestly Significant Difference test was used for post-hoc analyses of specific comparisons. These comparisons were 1) surface versus deep DO within each habitat type to determine strength of DO gradient in June and September, and 2) surface DO between habitat types in September. The surface stratum was chosen for between-habitat comparisons because it was consistently the highest DO throughout the water column.

Dissolved oxygen declined with month and depth over the 2012 summer season in all habitat types at Sandmine Lake (Figure 2-10). Surface-level DO was significantly higher than deep for all habitat types in June (Tukey HSD, $P<0.0001$), indicating a strong DO gradient. No hypoxia was seen in early summer. Low dissolved oxygen was first seen in August, with hypoxia extending throughout the entire water column in dense and edge habitat types. Dissolved oxygen declined to severe hypoxia in September with a very weak depth gradient, and surface DO was not significantly higher than deep

DO in any habitat type (Tukey HSD, *P*>0.05) during this month. This instance of hypoxia and severity declined in October.

Between-habitat comparisons of early morning DO in September 2012 showed mean surface concentrations in edge habitat type were not significantly higher than in dense habitat. Although hypoxia in open water habitat was less severe than in dense and edge habitat types, it did not differ significantly (Tukey HSD, *P*>0.05). Linear regression of dissolved oxygen from open water into dense hydrilla showed a strong relationship between open water and dense habitat dissolved oxygen concentrations at the deep and mid strata; however, the relationship between DO and distance to open water was weaker at the surface level due to the wider distribution in dense habitat (Figure 2-11).

Dissolved oxygen concentrations increased in the afternoon time period, such that DO reached the FDEP (2012) reviewed minimum (38% saturation, DO≥3.0 mgl^{-1} at 27.79°C) in the surface of the water column in all habitat types at Sandmine Lake (Figure 2-12). Mid-level DO varied by habitat type: DO remained severely hypoxic for both times of day in dense habitat, but edge saw DO rise from severe to stressful hypoxia, and open water maintained stressful hypoxia at the mid-level during both times of day. Dense and edge habitat types saw little change in deep-level hypoxia from dawn to dusk.

Temperature peaked at Sandmine Lake and Lake Tohopekaliga in July, and was less in September than in June (Table 2-4). Lake stratification by the temperature-density relationship was not seen through handheld sampling. Temperature changes with depth were generally small (<1.5˚C difference) in early summer and close to zero in late summer during early morning hours, Gradients were less than 1˚C difference in August and September for both years, suggesting little density stratification influence on dissolved oxygen concentrations during this time. A temporary gradient did occur in the afternoon with >1˚C difference from surface to bottom in afternoon periods at both lakes.

Since I did not detect hypoxia in June or July, there was no potential habitat limitation during these months (Figure 2-13). Hypoxia first occurred in August and peaked in September during early morning hours with 100% of the water column severely hypoxic in both, dense and edge habitat types. Open water maintained stressful conditions throughout the water column during this time. No potential habitat use limitation due to hypoxia was seen in any habitat type in October.

Lake Tohopekaliga

Dissolved oxygen did not decline to hypoxic concentrations at any time or depth in Lake Tohopekaliga during summer 2012 (Figure 2-14). There was a strong DO gradient in all habitat types in June (Tukey HSD, $P < 0.001$) which became very weak in September (Tukey HSD, $P > 0.05$). Although data collection was not possible in October, it is unlikely hypoxia occurred if it was not evident in September when hydrilla growth was at a maximum. Between-habitat comparisons for September showed mean surface DO did not vary significantly between any habitat types (Tukey HSD, $P > 0.05$). Because dissolved oxygen did not decline to hypoxic concentrations, there was no area of habitat loss for any habitat type. Dissolved oxygen concentrations were well above the level of hypoxia as well as the FDEP (2012) recommended minimum during both, early morning and afternoon time periods in all habitat types at Lake Tohopekaliga.

Vegetation Biomass

Hydrilla biomass maintained extremely high densities throughout the year at Sandmine Lake, with the lowest dry weight biomass density close to 1.5 kgm^{-2} a yearly average of 5.37 kgm^{-2} (n=80; Figure 2-15). Relative density of hydrilla was much higher at Sandmine Lake as compared with Lake Tohopekaliga. Samples were variable with the rake method; however, consistent method of collection allowed us to obtain relative density among months and between lakes.

Discussion

Complete hypoxia was not present for extended periods of time in hydrilla habitats at either system. Sampling on a microscale allowed us to detect areas of elevated oxygen within the dense hydrilla bed at Sandmine Lake, even when most of the habitat was severely hypoxic. These areas may provide temporary refuge for fish during times of poor water quality in late summer, as suggested by Miranda et al. (2000). Furthermore, even though the majority of the habitat was severely hypoxic, I did not see fish kills at any time. The natural, diel fluctuation of dissolved oxygen in aquatic environments rarely results in fish kill events unless compounded by other factors such as extreme weather conditions (Kramer, 1987), and my results suggest that hydrilla does not cause substantial impacts or limitation in habitat use except for short periods in late summer.

Contrary to my expectations, edge habitat did not exhibit significantly improved dissolved oxygen concentrations compared to dense habitat late in the summer season at Sandmine Lake. This contrasts with the study by Miranda and Hodges (2000), who found dense macrophyte beds to be severely hypoxic (DO <1.0 mgl^{-1}) and the edge to have slightly improved DO concentrations (DO 1.0-2.0 mgl^{-1}). The extensive hydrilla infestation at Sandmine Lake may have reduced water circulation in the open water and edge sampling areas (Carter et al., 1991; Miranda & Hodges, 2000). Miranda and Hodges (2000) found dissolved oxygen concentration in edge habitat to have a negative relationship with overall macrophyte coverage of the bay. Water circulation increases nutrient availability and promotes oxygen production by phytoplankton (Frodge et al., 1990; Fee et al., 1992). Maximum hydrilla growth and widespread matting throughout the lake resulted in minimal open water surface area, primarily found in the mining area that was too deep for substantial plant growth. If water movement is hindered by adjacent macrophyte beds, this could impact either open water or edge DO concentrations. This suggests that in order for edge habitat to have higher DO concentrations compared with dense hydrilla beds, adequate open water area must be maintained.

My results of biomass density and temperature at Sandmine Lake suggest other factors likely influence dissolved oxygen in this lake. I hypothesized that dissolved oxygen would decrease to hypoxic values due to high biomass density and high water temperature. However, biomass density at Sandmine Lake does not appear to have seasonal fluctuation, but maintains high densities consistently. Furthermore, temperature peaked earlier in the summer (July), and by September had decreased to less than that seen in June. If our hypothesis had been correct, we would have expected to detect hypoxia in July (when we had not), rather than September (when complete hypoxia occurred). This anomaly indicates that there must be another factor contributing to hypoxic conditions at Sandmine Lake.

Profuse branching and tangling of the canopy layer likely caused over estimation of vegetation biomass values per sediment area sampled. Regardless, it is evident that Sandmine Lake experiences little seasonal suppression of hydrilla growth. Due to limited senescence during winter months and warm temperatures arriving earlier in the season, shoots are able to reach the surface much earlier than in northern states where significant biomass reductions occur. The advanced development of the surface canopy consequently provides substrate for epiphytic algae earlier in the season, as well. Higher water temperatures can accelerate and compress the growth cycle of hydrilla so that senescence also occurs sooner in the growing season, releasing nutrients readily taken up by filamentous algae (Barko & Smart, 1981). Although I did not quantify it, it was common to see algal blooms on surface-matted hydrilla in late summer, and this was noted in dense hydrilla beds in both lakes in September. Algae blooms have considerable impact to dissolved oxygen concentrations, and this probably a significant factor in the dissolved oxygen dynamics of freshwater-hydrilla systems (Beer et al., 1986; Heffernan et al., 2010).

Greater water circulation in Goblet's Cove at Lake Tohopekaliga may help maintain adequate dissolved oxygen concentrations over the summer season. By September, 60% of the cove contained surface-matted hydrilla and temperatures were similar to those seen at Sandmine Lake, however no hypoxia was detected. Even with substantial hydrilla coverage, the increased size and fetch of Lake Tohopekaliga is capable of generating substantial wave action, which increases water circulation (Stewart, 1961). Water influx from a canal connecting Goblet's Cove to East Lake Tohopekaliga could also have influenced dissolved oxygen concentrations and reduced the chance of hypoxia occurrence, even though September sampling sites were 1.61 km from the canal discharge.

Although wide-spread hydrilla matting occurred at Lake Tohopekaliga in late summer, the biomass density was much less as compared with Sandmine Lake and may also facilitate better water circulation. Hydrilla beds at Sandmine Lake may have spatially-dense root crowns, potentially allocating growth energy to vertical stemming and surface branching. The gradual depth changes in Lake Tohopekaliga may allow hydrilla to lengthen rhizome growth between root crowns, taking advantage of horizontal expansion over vertical growth ("guerilla" strategy; McCreary, 1991). Furthermore, the fine sediment substrate at Sandmine Lake (silt, clay, and high amounts of organic build up) supports better hydrilla growth and decomposition than the sandy, shell bottom found at Lake Tohopekaliga (Cole, 1994; Smart et al., 2005; UF IFAS, no date). Reduced shoot density and canopy thickness allows deeper sunlight transmission for photosynthesis and better water circulation which can influence dissolved oxygen considerably. Comparison between these lakes shows that dissolved oxygen dynamics is significantly influenced by a number of factors, including lake size and fetch, hydrilla density, and the particular hydrodynamics of the study area.

Diel changes in DO during September at Sandmine Lake were substantial in dense and edge habitats. The dense hydrilla canopy caused wider fluctuations due to higher rates of photosynthesis and respiration as compared with photosynthetic phytoplankton in open water (Hannan & Anderson, 1971; Frodge et al., 1990; Fee et al,. 1992). Without the substantial increase in oxygen during the day, dissolved oxygen in dense hydrilla may never reach suitable concentration for fish habitation when complete hypoxia occurs during night/early morning hours.

Plant architecture is a significant factor in evaluating the quality of fish habitat and can vary greatly among SAV species (Lillie & Budd, 1992; Dibble et al., 1996a). Ideally, fish habitat contains high light levels for optimal foraging efficiency and vegetation photosynthesis, as well as a degree of structural complexity for macroinvertebrate attachment and protection from predators. Although >50% of complexity was concentrated in the upper strata (canopy), Dibble et al. (1996a) found hydrilla to have intermediate complexity and light attenuation, providing a balance of these two factors. High surface area associated with stems, leaves, and branches of hydrilla increases the abundance and diversity of macroinvertebrates and attracted fishes (Moxley & Langford, 1982). However, macrophyte complexity is positively correlated with nightly respiration rate, which can substantially impact dissolved oxygen concentrations and render this uninhabitable for fish (Caraco & Cole, 2002). My results of spatiotemporal dissolved oxygen dynamics in hydrilla are similar to that found by Frodge et al. (1990) and suggest that although hydrilla grows rapidly and densely, it does not impact dissolved oxygen more than other dense submergent species. Furthermore, it is evident that although some hydrilla beds experience hypoxic conditions in late summer, this is not non-native/invasive species-specific (Frodge et al., 1990; Moore et al., 1994; Caraco & Cole, 2002; Caraco et al., 2006). In fact, given the diel fluctuation of dissolved oxygen in SAV species such as dense hydrilla, coontail *Ceratophyllum demersum*, elodea *Elodea canadensis*, and southern naiad, this habitat structure may be more beneficial for fish utilization than floating-leaved species which have lower complexity and can experience prolonged hypoxia (Frodge et al., 1990; Moore et al., 1994; Miranda et al., 2000). Hydrilla can provide beneficial ecological services to freshwater macroinvertebrate and fish communities.

While hydrilla habitat provides plentiful food sources and protection from predatory species, these attributes become null if a suitable water quality standard is not met. Therefore, the value of hydrilla as quality habitat fluctuates over a large scale (seasonally) and small scale (hours), although my study clearly showed that this is lake or regionally-specific. Hydrilla in Goblet's Cove is probably of better habitat quality than dense beds found in Sandmine Lake due to the adequate dissolved oxygen levels throughout summer and reduced vegetation density. My study and others (Moxley & Langford, 1982; Dibble et al., 1996b) suggest that hydrilla is generally beneficial fish habitat, and management should focus efforts toward angler and recreational boater expectations while maintaining some vegetation coverage for fish population utilization.

Further study of fish community behavior and tolerance of adverse conditions in the natural environment would be informative for aquatic plant management decisions and strategies, as the occurrence of hypoxia over the summer season may impact how fish utilize these habitats spatially and temporally (Suthers & Gee, 1986; Miranda et al., 2000; Troutman et al., 2007). Fish alter their behavior when confronted with hypoxia by changing activity (reduced swimming rate and/or increased gill ventilation rate), air breathing (in bimodal species), increasing aquatic surface respiration, or by selecting new habitat with better conditions (Kramer, 1987). Fish migration from hypoxic habitat or tolerance of low DO may depend on the severity of hypoxia, fish species, or fish size (Barnett & Schneider, 1974; Miranda & Hodges, 2000). Remaining in vegetation or moving from the hypoxic area can lead to overcrowding, decreased growth, and lower survival if adequate habitat is limited and fish become concentrated (Eby et al., 2005). Given my results of hypoxia throughout the water column except for the surface canopy in the afternoon, overcrowding in this stratum may be a concern (Haller et al., 1980).

It is likely that smaller fishes (i.e., sunfish) utilize dense aquatic plant habitat more often than large predatory species (i.e., largemouth bass), which may prefer edge habitat (Barnett & Schneider, 1974; Miranda & Hodges, 2000). Smaller fish require less oxygen than their larger counterparts. If smaller fishes are better able to manage hypoxia or possess coping mechanisms for low DO encountered seasonally in the environment, they may not be excluded from this habitat and vegetation removal may not be necessary. Ultimately, organisms will opt for whichever strategy requires the lowest energy expenditure, weighing the cost of migration, food resources, and risk of predation (Kramer, 1987).

Investigation of dissolved oxygen dynamics across lakes would be beneficial to understand the variation of DO impacts by hydrilla. In this study, I looked at a very small lake with a hydrilla infestation that is likely a worst-case scenario. It would be informative to investigate the DO dynamics of a moderate hydrilla infestation. Additionally, study of other areas of Lake Tohopekaliga would also help prevent making broad conclusions about DO dynamics in this lake, particularly given the likely influence of the eastern canal off of Goblet’s Cove.

Determination of minimum open-water area size for adequate water circulation to improve dissolved oxygen concentrations on edges or within dense hydrilla beds is needed. If dissolved oxygen within the interior of dense macrophyte beds is low, improved water quality on edges provides alternative habitat for fish use, alleviating potential overcrowding in microrefuges or the surface stratum (Haller et al., 1980; Trebitz & Nibbelink, 1996). Aside from improved water quality, increasing ecotonal habitat can promote macroinvertebrate and fish communities with increased foraging and benefit recreational boaters for navigation (Lillie & Budd, 1982; Trebitz & Nibbelink, 1996; Olson et al., 1998). With recent advances in GPS and deep-water mechanical removal of dense macrophytes, longer-term control in channels due to decreased light transmission may now be a possibility (Haller & Jones, 2012).

Finally, the variation between sampling methods shows how different tools can greatly change the assessment of our environment. The difference between handheld water quality meters and remote data loggers is obvious: while autonomous water quality recorders can be left for long periods of time, it does not obtain the spatial resolution to sufficiently describe microhabitat conditions. It is thus difficult to establish the extent of poor water quality, particularly in heterogeneous environments. Because the descriptive statistics of the habitat types were systematically obtained from time series data, the means represent an average of the night/early morning period; conversely, handheld data means represent an average of the early-morning minimum. Even with handheld water quality meters, studies rarely obtain enough data points to accurately reflect the microspatial scale of water quality parameters in a variable habitat type. The tools and study design scientists implement can largely influence how we perceive our environment. Prior to field research, clear objectives should be made to determine what methods are most appropriate for data collection.

Severe hypoxia was present only in Sandmine Lake and for a limited period of time in late summer, which may not substantially impact growth and survival of fish populations. If management is required, macrophyte removal may only be needed for short, limited periods during late summer. Submersed macrophytes provide valuable resources and support higher fish abundance and diversity than open water areas (Barnett & Schneider, 1974; Killgore et al., 1989). This habitat should be managed in a way to maintain some macrophyte coverage but also improve the overall ecosystem condition.

Table 2-1. Mean distance (meters) between sampling locales (n=4 for each habitat type) at Sandmine Lake and Lake Tohopekaliga, summer 2012, where “D” is dense habitat type, “E” is edge habitat type, and “OW” is open water habitat type.

	Sandmine Lake			Lake Tohopekaliga		
	D-E	E-OW	D-OW	D-E	E-OW	D-OW
Jun	20	31	49	50	56	104
Jul	29	38	70	42	41	80
Aug	25	36	53	81	111	182
Sep	25	29	48	101	142	229
Mean	24.8	33.5	55.0	68.5	87.5	148.8

Table 2-2. Descriptive statistics of dissolved oxygen concentrations from time series data at Sandmine Lake, September 15-24 2011, where n=60.

Habitat	Depth	Mean	SE	Min	Max
Dense	Surface	2.28	0.36	0.88	3.39
	Mid	0.50	0.18	0.07	1.19
Edge	Surface	1.60	0.43	1.08	4.76
	Mid	0.64	0.17	0.23	1.37
Open water	Surface	4.83	0.77	2.68	7.37
	Mid	3.00	0.47	1.76	4.65

Table 2-3. Analysis of variance table for early morning data, summer 2012, Sandmine Lake and Lake Tohopekaliga.

Source	Df	Sum Sq.	Mean Sq.	F value	Pr(>F)
Month	3	1246.20	415.41	214.87	<0.0001
Habitat	2	11.70	5.83	3.02	0.049
Depth	2	564.50	282.23	145.98	<0.0001
Lake	1	1321.50	1321.51	683.53	<0.0001
Month:Habitat	6	38.60	6.43	3.32	0.003
Month:Depth	6	381.10	63.51	32.85	<0.0001
Habitat:Depth	4	30.70	7.68	3.97	0.003
Month:Habitat:Depth	12	59.70	4.98	2.57	0.002
Residuals	1763	3408.50	1.93		

Table 2-4. Monthly temperature (°C) gradients during early morning and afternoon hours at Sandmine Lake and Lake Tohopekaliga, June – October 2012. Values are means from handheld sampling events, all n=25 except September at Sandmine Lake where n=15.

		Early morning			Afternoon		
Lake	Month	Surface	Deep	ΔT (°C)	Surface	Deep	ΔT (°C)
Sandmine	Jun	27.70	26.76	0.94	31.09	26.78	4.31
	Jul	28.65	25.54	3.11	30.51	28.63	1.89
	Aug	27.81	27.71	0.10	30.12	27.64	2.48
	Sep	26.74	26.74	0.00	28.72	26.98	1.74
	Oct	23.07	23.14	-0.07	nd	nd	nd
Tohopekaliga	Jun	28.30	27.91	0.39	31.22	28.83	2.39
	Jul	29.45	29.18	0.27	31.81	28.97	2.84
	Aug	28.59	28.49	0.10	29.69	29.18	0.51
	Sep	27.83	27.81	0.02	29.05	27.95	1.10

nd= no data

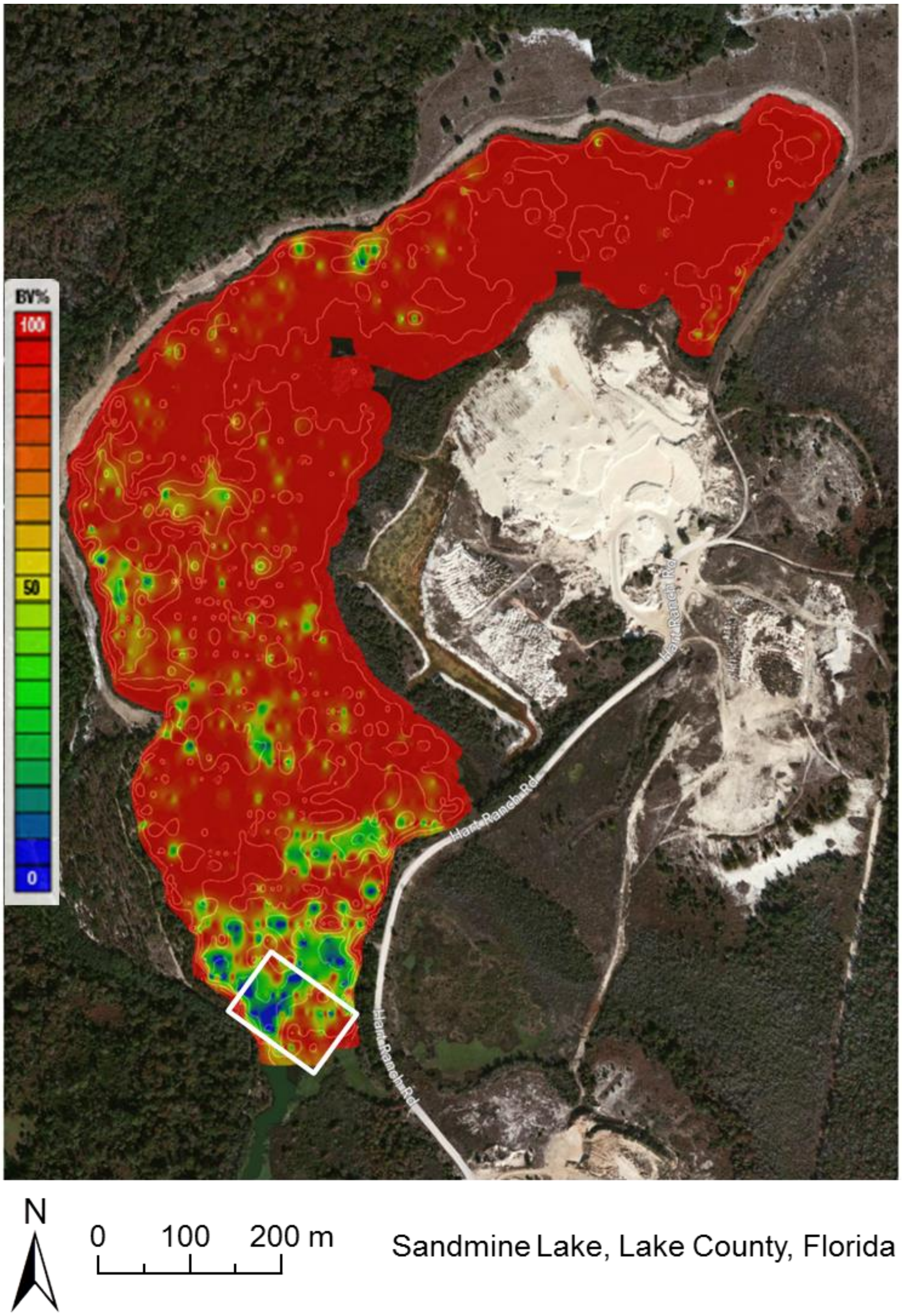


Figure 2-1. Vegetation coverage map of Sandmine Lake, Lake County, Florida, within the Lake Norris Conservation Area, March 2012. The white box represents the primary sampling areas of summers 2011 and 2012.

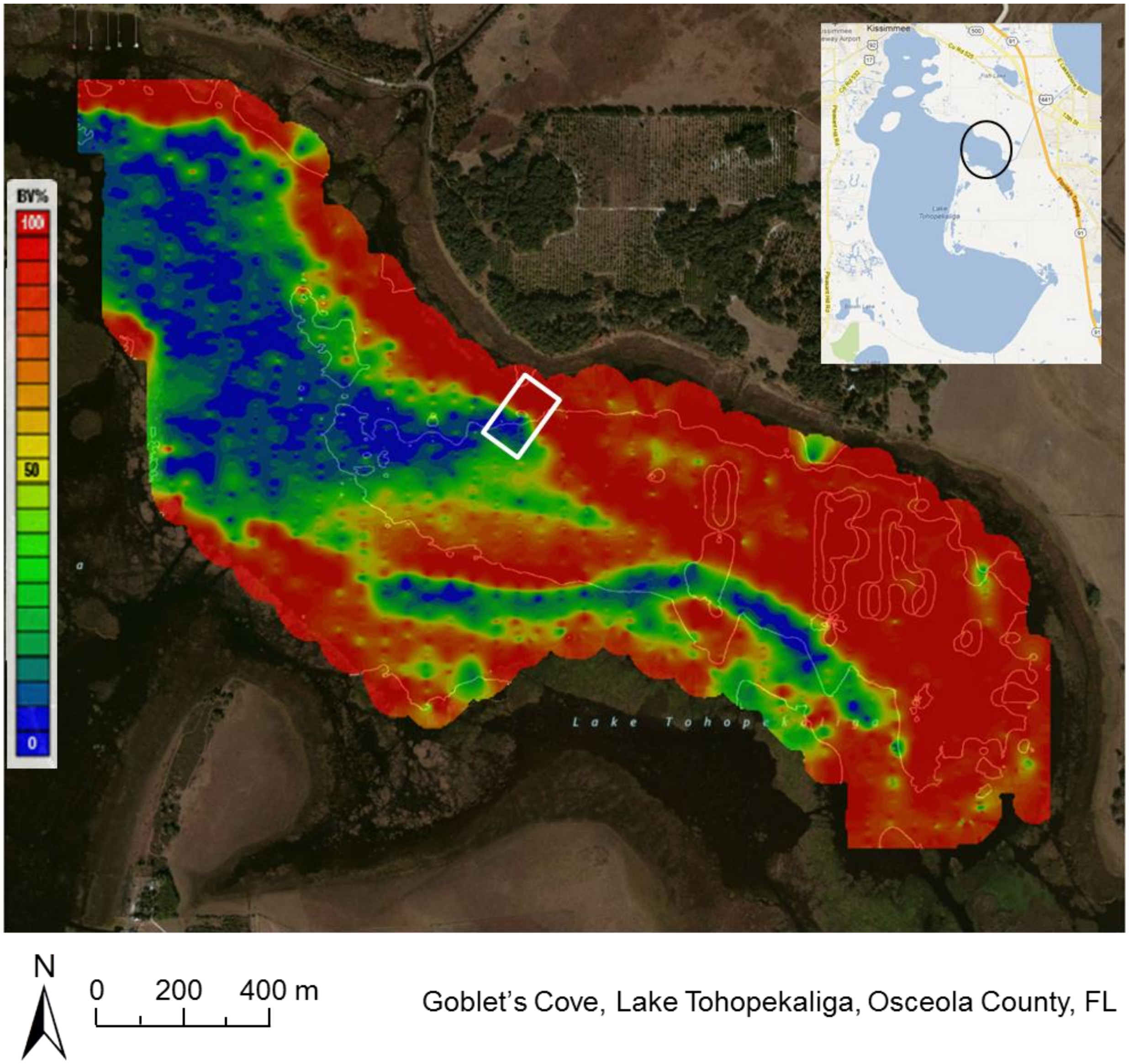


Figure 2-2. Vegetation coverage map of Goblet's Cove, Lake Tohopekaliga, Osceola County, Florida, September 2012. The white box represents the handheld sampling area. Locator map obtained from maps.google.com.

Figure 2-3. Surface-matting dense hydrilla at Sandmine Lake, Lake County, Florida, September 2012.

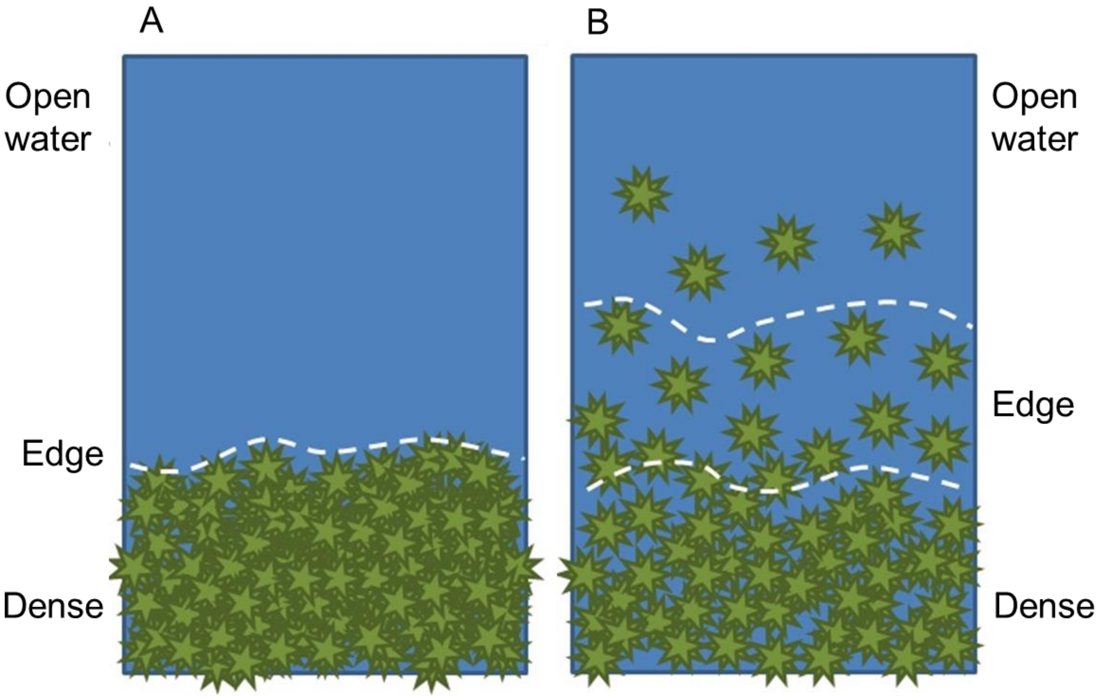


Figure 2-4. Schematic depicting differences in edge habitat type between A) Sandmine Lake and B) Lake Tohopekaliga, summer 2012.

Figure 2-5. Vertical rake used for hydrilla biomass collection for relative density samples (Johnson and Newman 2011).

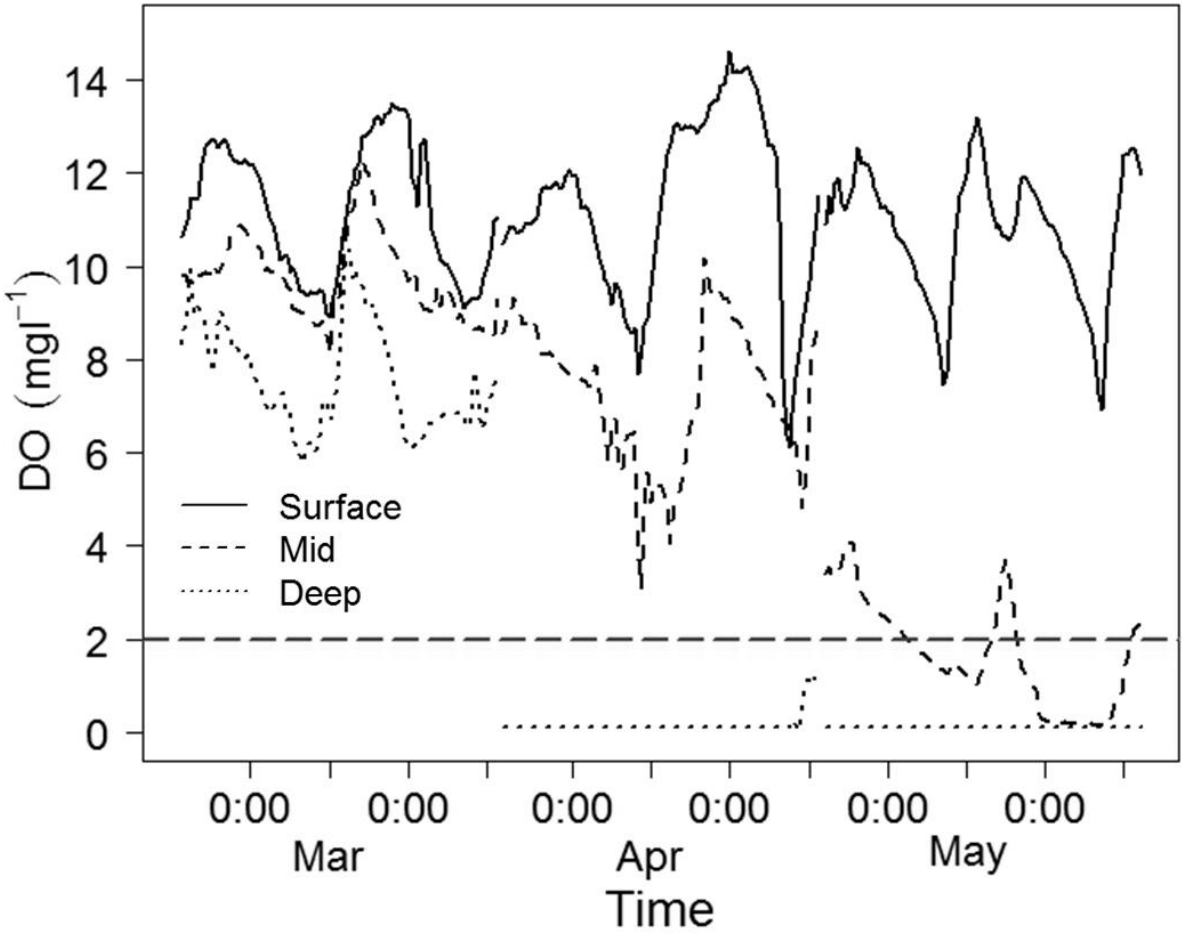


Figure 2-6. Dissolved oxygen concentrations recorded every 30 minutes over 2 days in dense habitat type by surface, mid, and deep depths at Sandmine Lake, March – May 2011. Long-dashed line set at 2.0 mgl^{-1} represents the threshold of hypoxia and white bars are periods of sunlight.

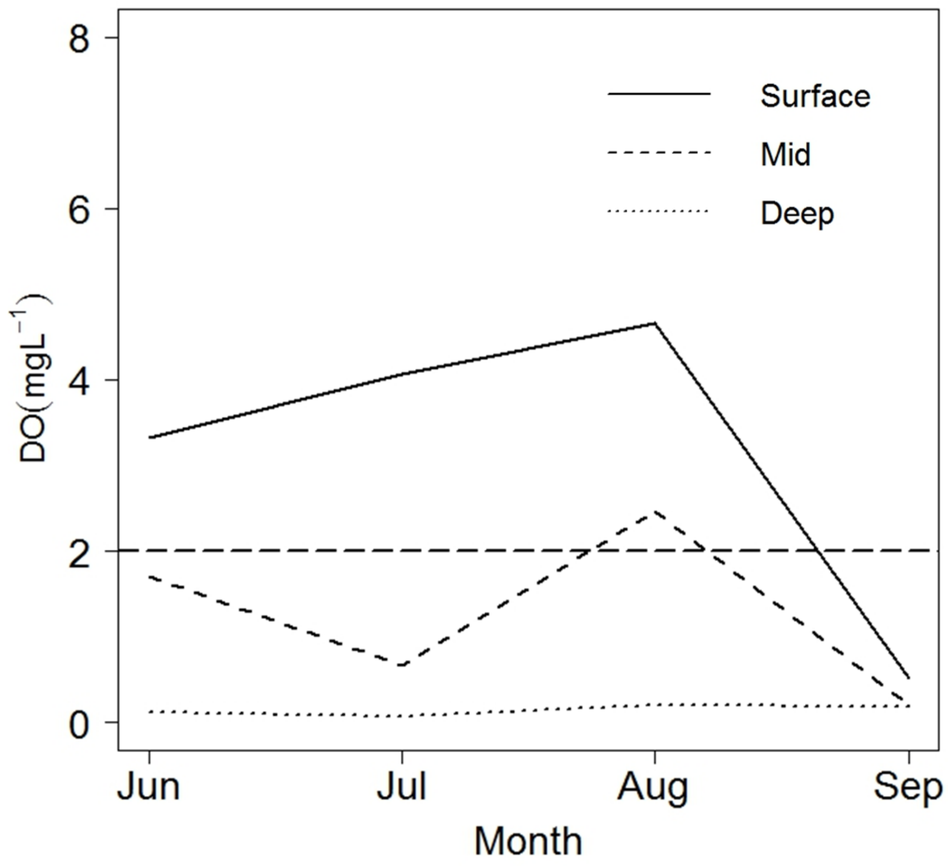


Figure 2-7. Mean early morning dissolved oxygen concentrations (n=25) of dense hydrilla beds by depth and month at Sandmine Lake, June – September 2011. Long-dashed line set at 2.0 mgl^{-1} represents the threshold of hypoxia.

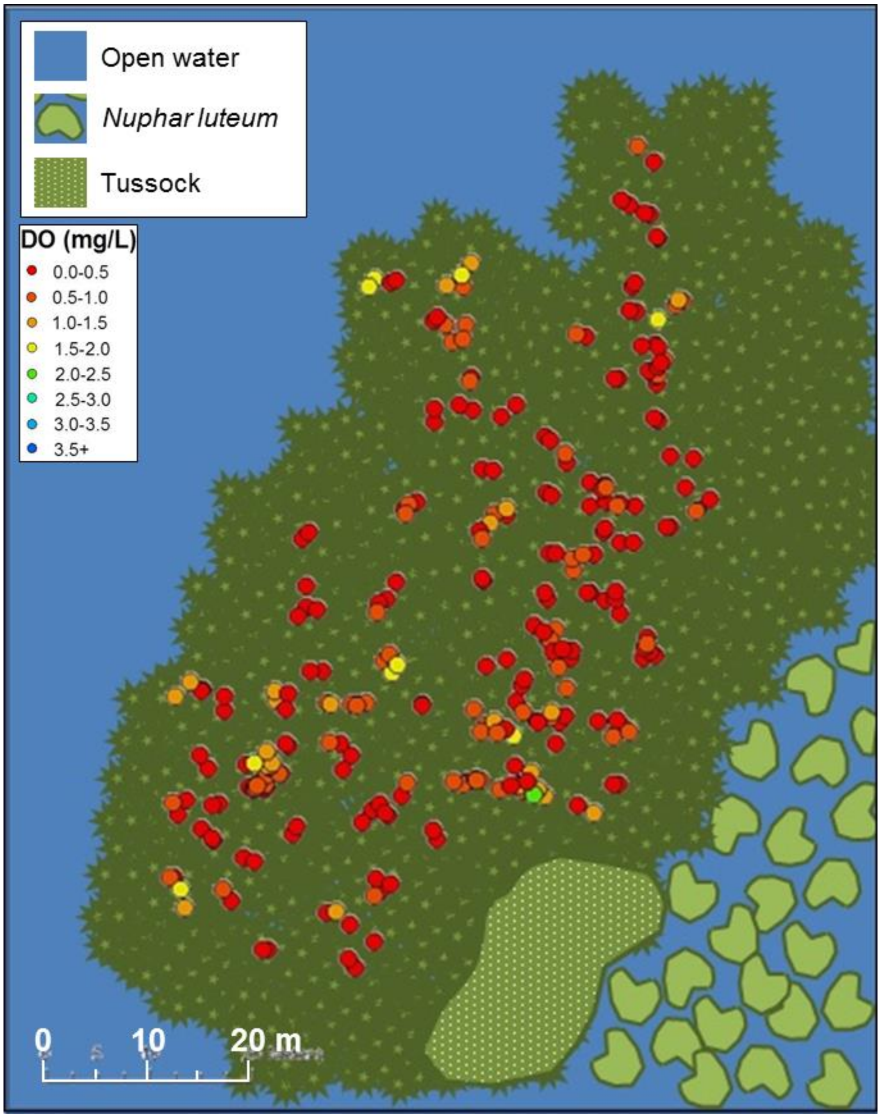


Figure 2-8. Schematic of spatial distribution of handheld dissolved oxygen readings (n=280) at the surface level of dense hydrilla beds during early morning hours over five days at Sandmine Lake, September 2011.

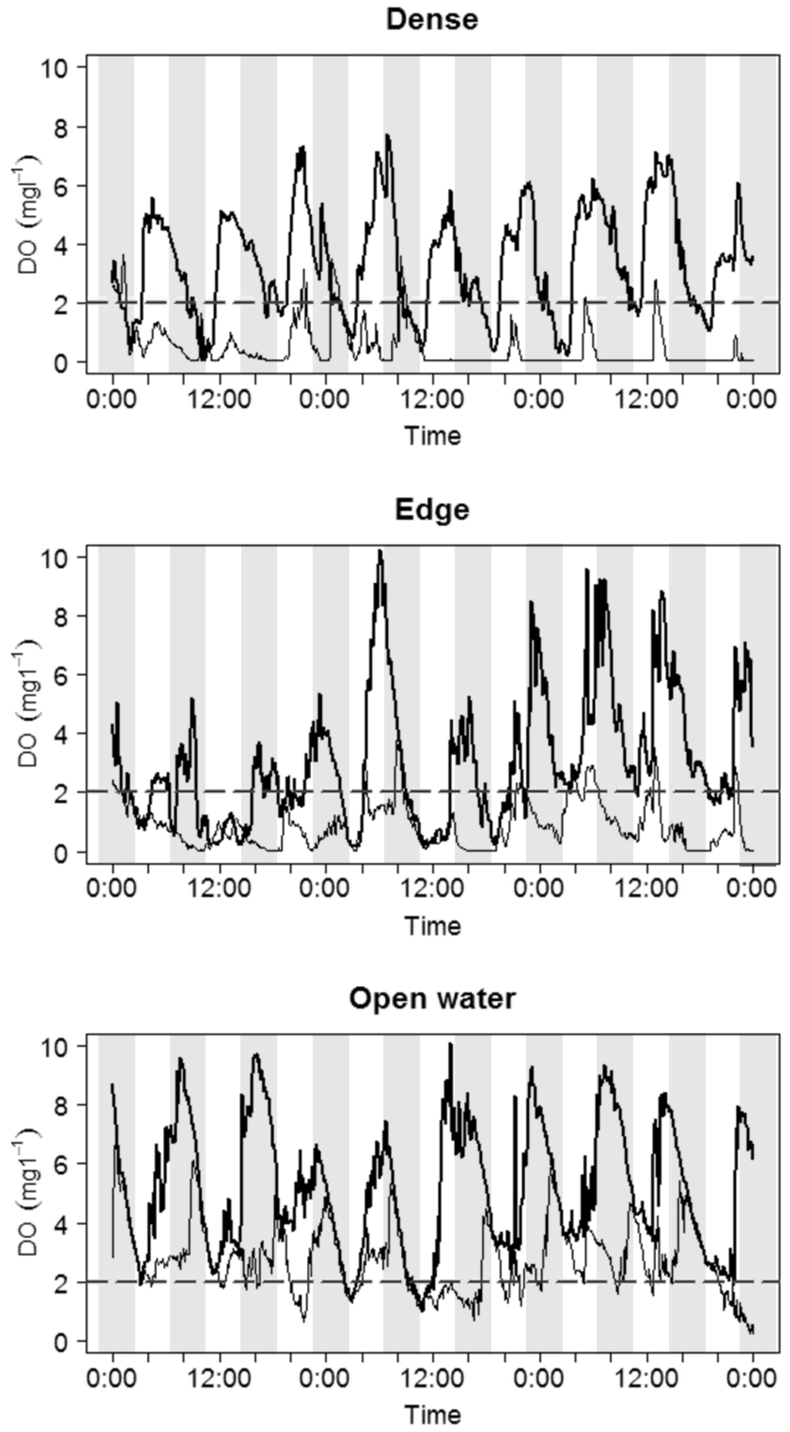


Figure 2-9. Dissolved oxygen concentrations recorded every 15 minutes for 10 days in Dense, Edge, and Open water habitat types by surface (bold line) and mid (thin line) depths at Sandmine Lake, September 2011. Long-dashed line set at 2.0 mgl^{-1} represents the threshold of hypoxia. Light bars are periods of sunlight.

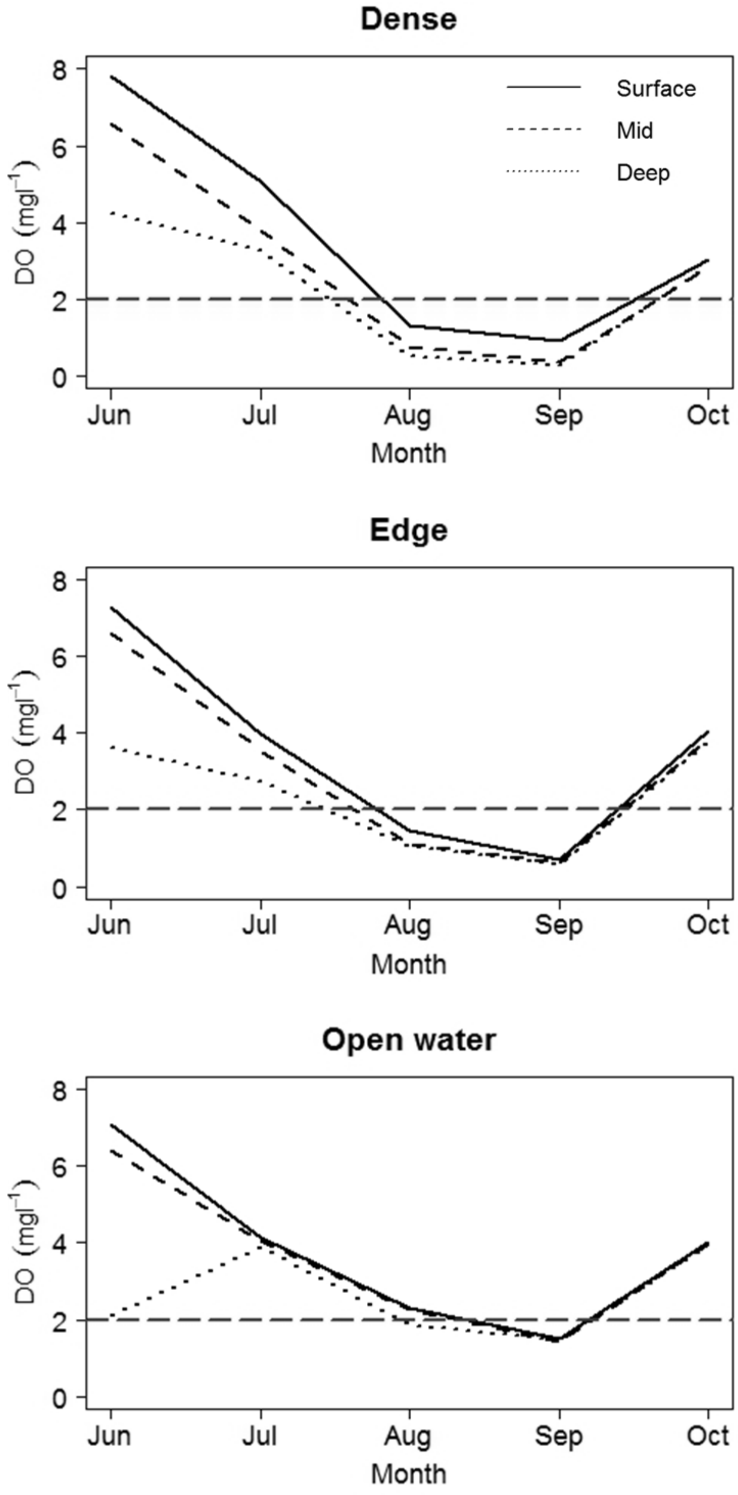


Figure 2-10. Early morning mean dissolved oxygen concentrations (All n=25 except n=12 for October) for Dense, Edge, and Open water habitat types by depth and month at Sandmine Lake, June – October 2012. Long-dashed line set at 2.0 mgl^{-1} represents the threshold of hypoxia.

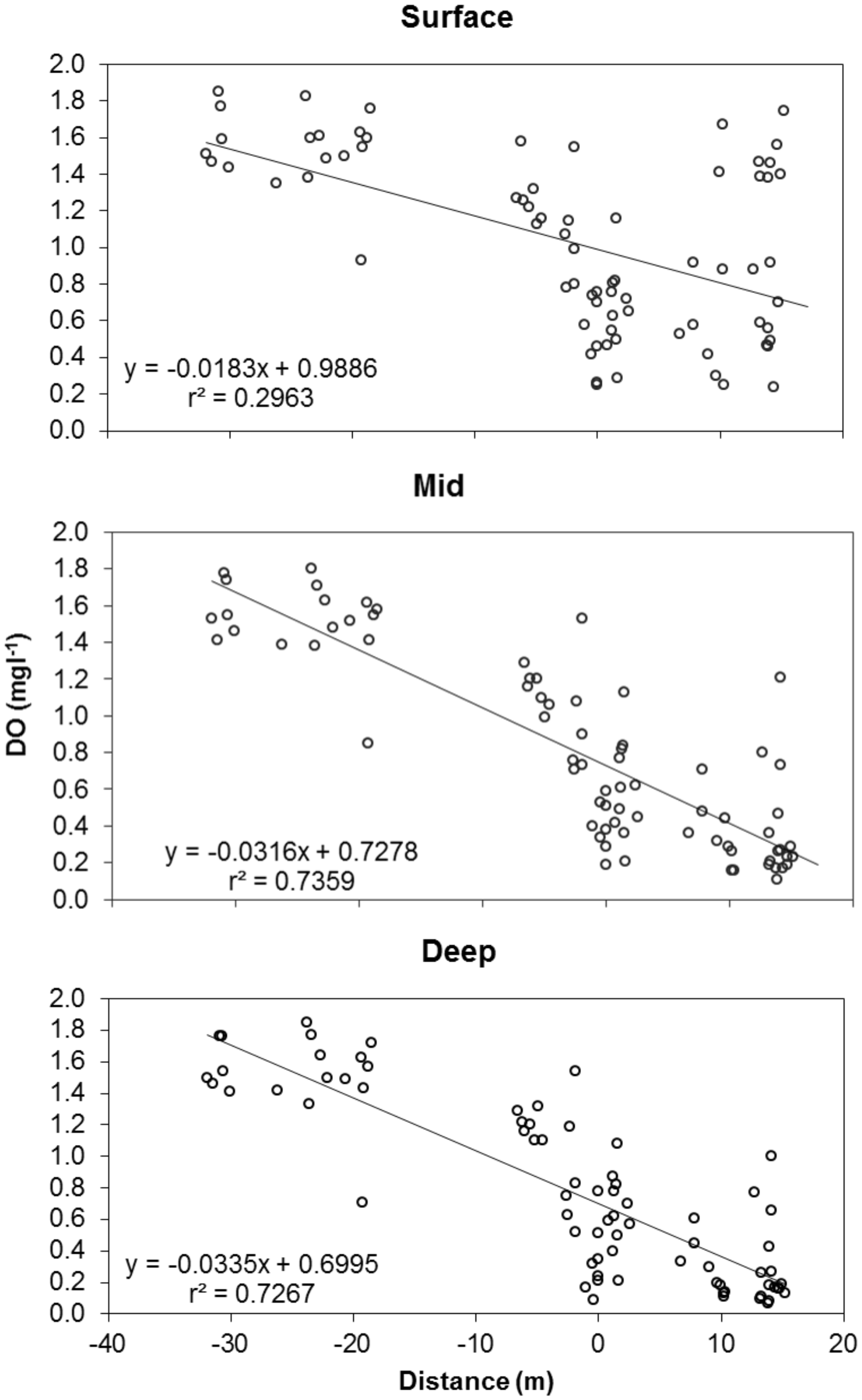
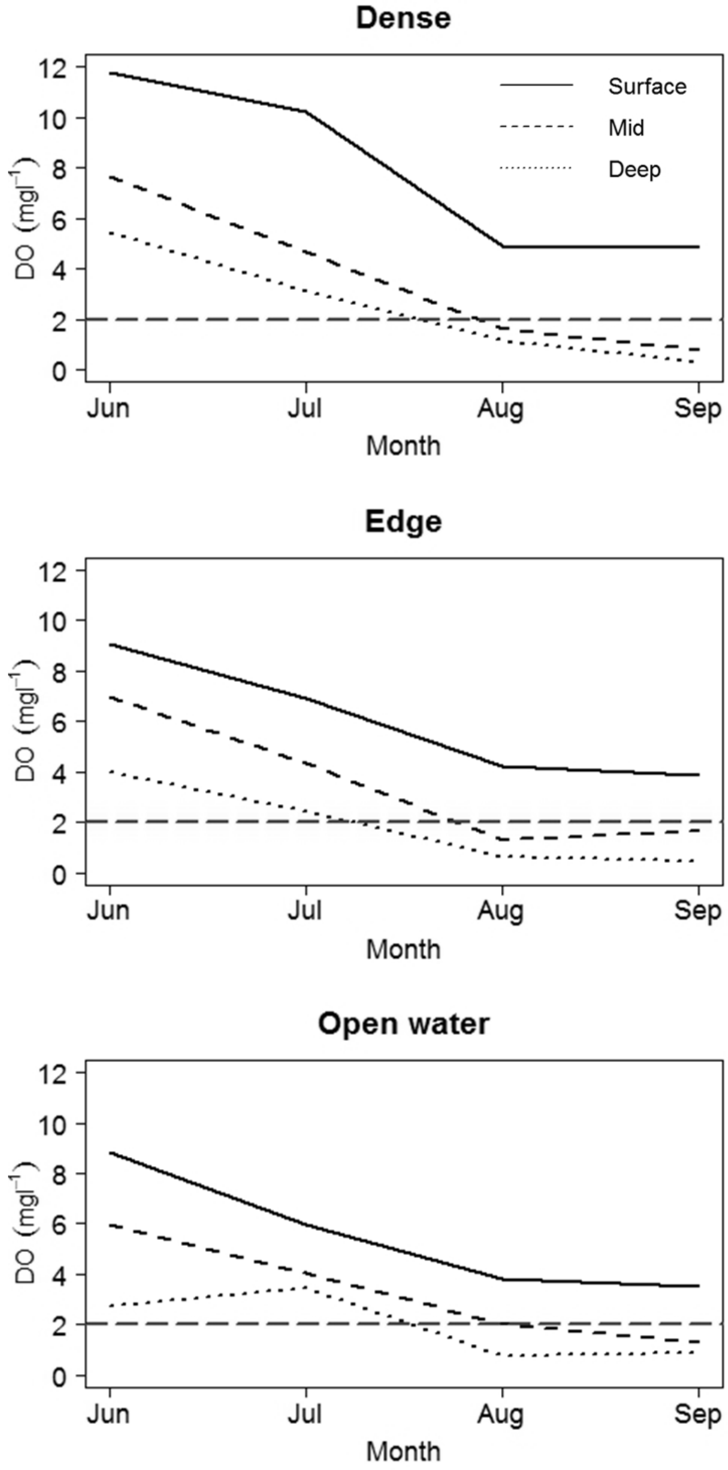


Figure 2-11. Linear regression of dissolved oxygen concentration (n=75) vs. distance from open water (negative values) into dense hydrilla bed (positive values), where edge = 0 m, at Sandmine Lake, September 2012. Surface, mid, and deep water strata are shown.



Dense

Edge

Open water

Figure 2-12. Afternoon mean dissolved oxygen concentrations (n=25) for dense, edge, and open water habitat types by depth and month at Sandmine Lake, June – September 2012. Long-dashed line set at 2.0 mgl^{-1} represents the threshold of hypoxia.

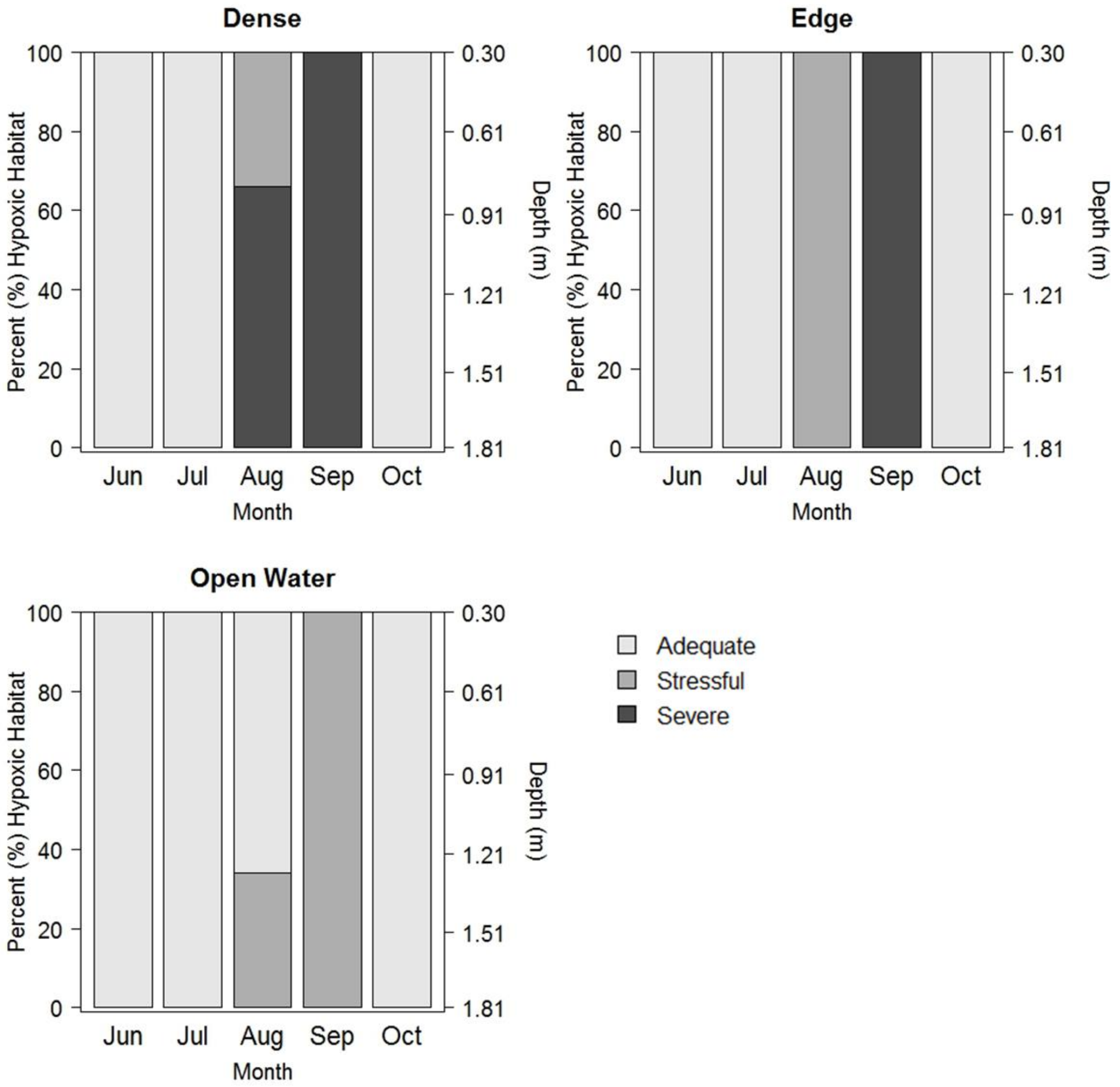


Figure 2-13. Early morning percent hypoxic habitat in dense, edge, and open water habitat types, Sandmine Lake, June – October 2012.

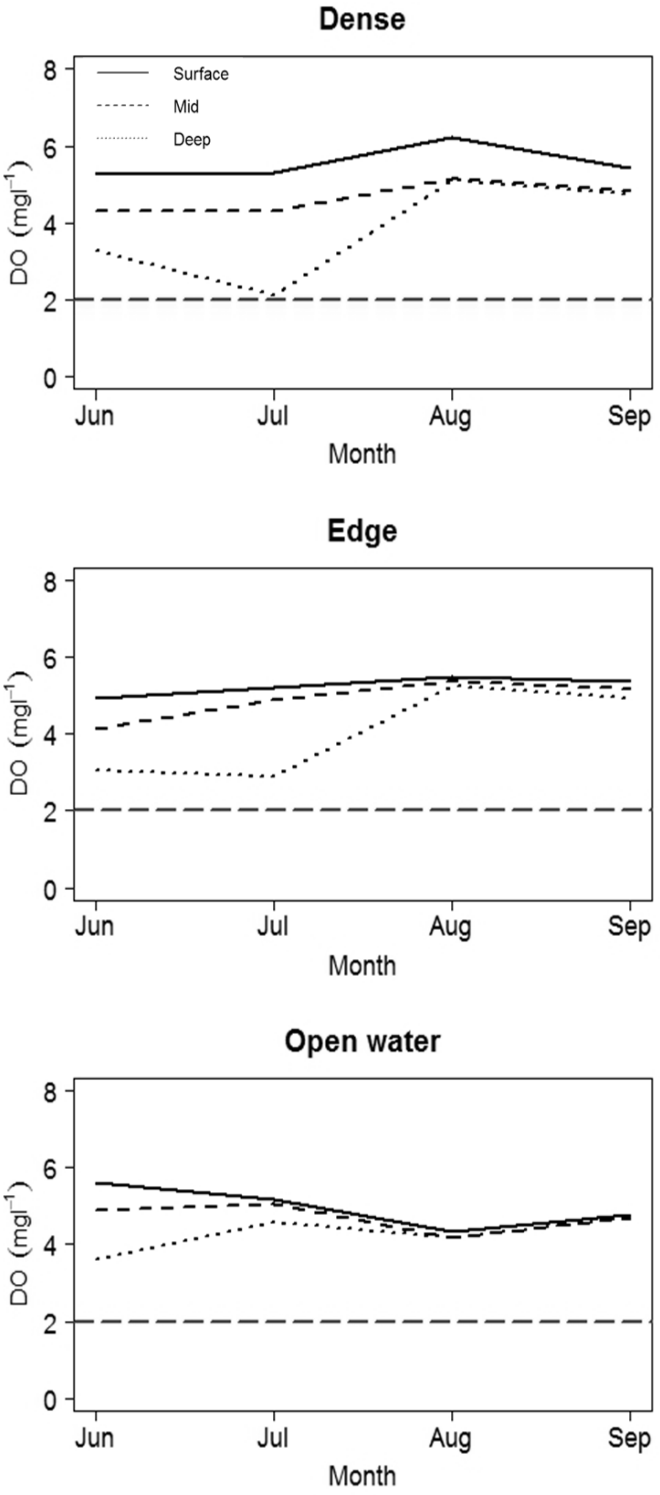


Figure 2-14. Early morning mean dissolved oxygen concentrations (n=25) for dense, edge, and open water habitat types by depth and month at Lake Tohopekaliga, June – September 2012. Long-dashed line set at 2.0 mgl^{-1} represents the threshold of hypoxia.

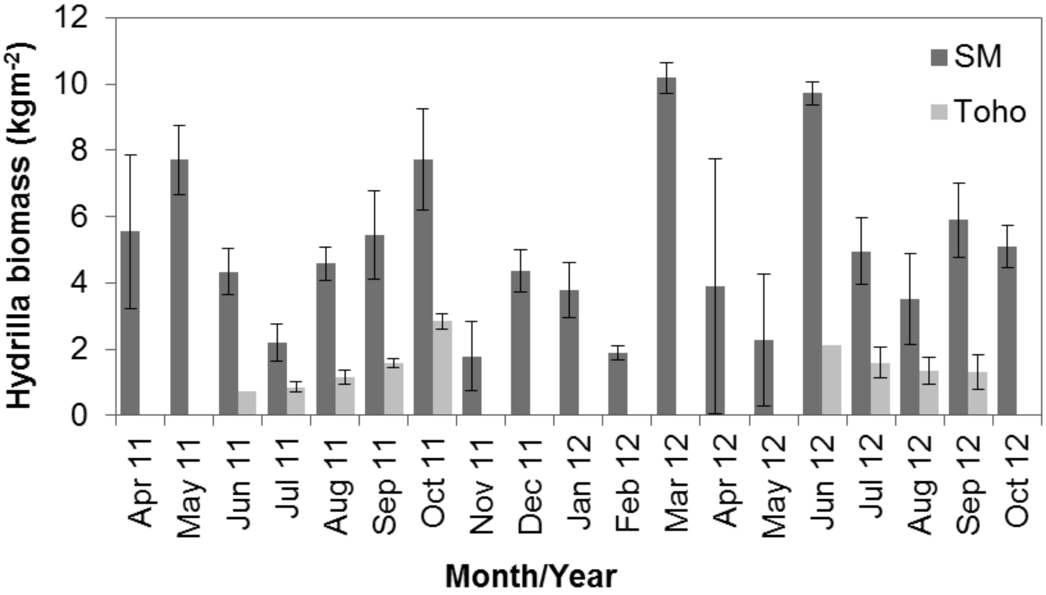


Figure 2-15. Hydrilla dry weight biomass (kgm^{-2}) samples (n=4) collected from Sandmine Lake and Lake Tohopekaliga 2011-2012. Bars are standard error bars.

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BIOGRAPHICAL SKETCH

Erin Bradshaw Settevendemio grew up in Peru, New York, just outside of the Adirondacks on Lake Champlain. After graduation from high school, she attended the State University of New York studying biology/ecology. As an undergraduate, she was had the opportunity to partake in the Applied Environmental Science Program, intern for the Lake Champlain Research Institute, and conduct an independent study assessing small mammal assemblages. Following graduation, she moved to southern Nevada for an AmeriCorps position as an Ecological Technician at Ash Meadows National Wildlife Refuge. There, she regularly trapped aquatic invasive species, monitored endangered fish populations, and helped restore unique desert spring ecosystems. When she finished her term position, she headed back across the country to the southeast, where she began as a fisheries technician in the Allen Lab. Working in the Allen Lab greatly expanded her experiences including bony fish structure ageing and radio telemetry, and she was very excited to begin her graduate education. The next two years were centered on her research evaluating the dissolved oxygen dynamics in dense aquatic weeds and learning invaluable lessons about experimental design and scientific writing. Following graduation, she is looking forward to obtaining a biologist position so that she can help make beneficial management decisions for natural resources and all the people who enjoy them.