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An evaluation of emergent macrophytes and use among groups of aquatic taxa

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Abstract

Aquatic vegetation serves an important ecological role. Previous research on the interactions of macrophytes and aquatic organisms has focused primarily on submersed macrophytes due to their structural complexity and associated ecological impacts. However, the role of emergent vegetation is far less understood and often overlooked because they lack structural complexity. We evaluated 3 common emergent macrophytes and an open water habitat, and determined use among multiple aquatic taxa. Pelican Lake, Nebraska, USA, served as our study system because it is dominated by 3 emergent macrophytes: common cattail (*Typha latifolia*), softstem bulrush (*Schoenoplectus tabernaemontani*), and common reed (*Phragmites australis*). Juvenile fishes (yellow perch [*Perca flavescens*] and bluegill [*Lepomis macrochirus*]), zooplankton, and benthic macroinvertebrates were sampled concurrently in each habitat patch over 3 months (Aug, Sep, and Oct). We identified few clear or consistent overall patterns in habitat use among emergent vegetation species across these aquatic taxa. However, bluegill and some zooplankton taxa were more abundant in emergent vegetation compared to open water habitats. Conversely, habitat use for some macroinvertebrate taxa differed among emergent vegetation species. Our results suggest that managers could select from a variety of emergent vegetation species to address management objectives, while also balancing ecological and social tradeoffs.

Keywords: Emergent macrophytes, habitat, juvenile fishes, lakes, macroinvertebrates, zooplankton

Aquatic vegetation provides many benefits to aquatic ecosystems. Macrophytes reduce shoreline erosion and turbidity levels, increase water quality (Madsen et al. 2001), and can serve both as a nutrient sink or source (Carpenter and Lodge 1986). Macrophytes also provide habitat for many aquatic organisms, including fishes, macroinvertebrates, and zooplankton. Leaves and stems of aquatic vegetation provide ideal surfaces for algae colonization, which can lead to higher abundances of zooplankton and macroinvertebrates (Dibble et al. 1996, Collingsworth et al. 2009, Strakosh et al. 2009). Zooplankton inhabit macrophytes during daytime hours as predation refuge from zooplanktivores such as juvenile fishes (Lauridsen et al. 1996, Cazzanelli et al. 2008). Juvenile fishes can also use aquatic vegetation as a refuge from predators (Savino and Stein 1982, Stahr and Shoup 2015) and may find abundant prey resources within these macrophyte patches (Crowder and Cooper 1982, Savino and Stein 1982). However, high densities of macrophytes can lead to decreased foraging efficiency and growth of some juvenile fishes (Gotceitas 1990, Harrel and Dibble 2001). Because macrophytes provide habitat for fishes, macroinvertebrates, and zooplankton, aquatic vegetation can ultimately play a large role in structuring food webs within the littoral zones of aquatic systems (Carpenter and Lodge 1986).

Although the role of macrophytes has been widely explored, most of these previous studies have focused on submersed macrophytes as opposed to emergent macrophytes. Much focus has been given to submersed macrophytes primarily because of their structural complexity and corresponding ecological benefits (e.g., Savino and Stein 1982, Jeppesen et al. 1997, van Donk and van de Bund 2002, Li et al. 2010). In contrast, emergent macrophytes are widely regarded as less structurally complex because complex growth typically occurs above the water's surface and is not accessible by many aquatic organisms. Multiple studies have concluded that more structurally complex submersed macrophytes provide better predation refuge for juvenile fishes (Savino and Stein 1982, Gotceitas and Colgan 1989). In addition, more structurally complex macrophytes can lead to higher invertebrate abundance (Warfe and Barmuta 2006, Walker et al. 2013). Due to the simple structural complexity of emergent macrophytes, it is hypothesized that all emergent macrophytes provide homogenous habitat and serve a similar function for many trophic levels. However, empirical data from field studies is lacking and it remains uncertain if all emergent macrophytes provide the same benefits to aquatic organisms. These organisms could colonize in different areas or reaches and occur in different densities. Therefore, more information is needed on the role of emergent macrophytes in structuring littoral habitats.

Emergent macrophytes serve many important roles in aquatic ecosystems. However, emergent macrophytes can occur in higher densities than submersed macrophytes in shallow, natural lakes. Cazzanelli et al. (2008)

noted that emergent vegetation may play a large role in ecosystem processes by creating predation refuge for zooplankton, leading to a decrease in algae and an increase in water clarity. In addition, some studies have found submersed and emergent macrophytes to be alike in invertebrate abundance (Van de Muetter et al. 2008) while others have identified differences in invertebrate assemblages between emergent and submersed macrophytes (Dvůrak and Best 1982). Emergent macrophytes may also play a large role in the recruitment dynamics of some fishes by providing critical refuge habitat and access to zooplankton prey during the juvenile life stage (Conrow et al. 1990, Bryan and Scarnecchia 1992). For example, plantings of emergent macrophytes for juvenile fish habitat are important in turbid reservoir systems where submersed macrophytes are difficult to establish (Strakosh et al. 2005, Collingsworth et al. 2009, Stahr and Shoup 2015). Radomski and Goeman (2001) also noted a decrease in the average size and biomass of some fishes when emergent macrophyte coverage was low. However, little information is available regarding aquatic habitat use among emergent vegetation species, in spite of their importance.

The objective of this study was to evaluate patterns of use by 2 juvenile fish species, benthic invertebrates, and zooplankton among 3 common emergent vegetation species and an open water habitat. These patterns were examined in a shallow, natural lake, across multiple months to account for habitat shifts that typically occur among fishes (e.g., Werner and Hall 1988). More specifically, we were interested in the functional response by each taxonomic group (juvenile fishes, macroinvertebrates, and zooplankton) with respect to each emergent vegetation species. Abundances and patterns of each taxonomic group should be comparable across vegetation species if similar interactions or functional roles are provided by each vegetation species (Van de Muetter et al. 2008, Collingsworth and Kohler 2010). Alternatively, contrasting patterns should emerge if interactions or functional roles differ among emergent vegetation species.

Materials and methods

Study site

Pelican Lake is a 332 ha, shallow (mean depth = 1.3 m) natural lake located in the Sandhills region of Nebraska, within the Valentine National Wildlife Refuge (Fig. 1). Pelican Lake is unusual in that it is primarily dominated by emergent macrophytes as opposed to submersed macrophytes. In addition, nearly all of the emergent macrophyte coverage in Pelican Lake is derived from 3 emergent aquatic plant species: common reed (*Phragmites australis*), softstem bulrush (*Schoenoplectus tabernaemontani*), and common

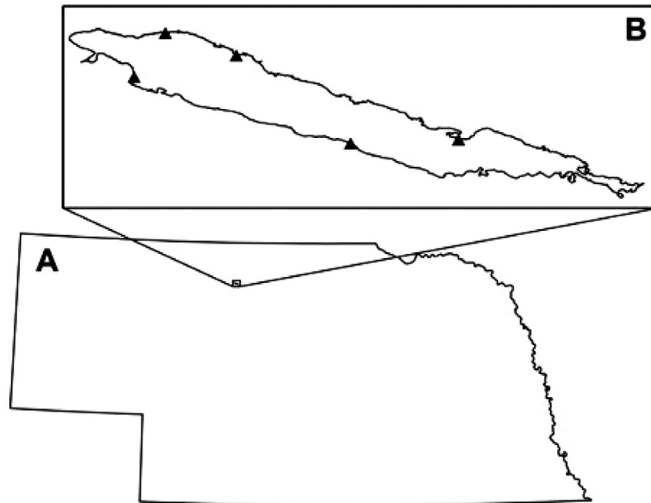


Figure 1. Location of study site; Nebraska, USA (A) and Pelican Lake (B). Triangles denote sites sampled during study.

cattail (*Typha latifolia*; hereafter referred to as reed, bulrush, and cattail, respectively). Using methods previously used for Sandhills lakes (Paukert et al. 2002), emergent vegetation coverage during late July 2009 in Pelican Lake was 8.5% for reeds, 15.5% for bulrush, and 7.0% for cattails (31% total emergent vegetation coverage). The remaining portion of the lake was classified as submersed vegetation (9.9%) and open water (59.1% [void of vegetation]). Total phosphorus and chlorophyll *a* levels ranged from 0.11 to 0.38 mg/L (mean = 0.20 mg/L) and 17.6 to 254.0 $\mu\text{g/L}$ (mean = 81.0 $\mu\text{g/L}$), respectively, during August 2004–2012 (Kaemingk MA, unpubl. data). The fish assemblage is composed of bluegill, yellow perch, largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), black bullhead (*Ameiurus melas*), common carp (*Cyprinus carpio*), and fathead minnow (*Pimephales promelas*; Wanner 2011).

Habitat use and sampling

Five sampling sites were selected that represented different areas of the lake (Fig. 1). Within these sites, 4 different habitat patches were present. Sites were identified based on the criterion that all 4 habitat patches were within a 50-m radius to minimize spatial variation among samples (Kaemingk and Willis 2012). Thus, not all habitat patches were entirely within this radius but included the sampled interior of each patch. Habitat patches were categorized (>90% relative frequency) as (1) reed, (2) bulrush, (3) cattail, or (4) open water (lacking both emergent and submersed vegetation; Kaemingk

and Willis 2012). Habitat patches were sampled across all sites during August, September, and October of 2009 in Pelican Lake (4 patches \times 5 sites = 20 samples/mo, excluding fish sampling).

Vegetation coverage (VC score) was measured at each patch and reflected overall vegetation coverage and distribution (Murry and Farrell 2007, Stahr et al. 2013; see Table 1 for more details). VC scores allow characterization of both density and distribution of vegetation among habitat patches, with greater coverage reflecting higher density and more homogenous distribution of stems throughout the patch. Quantifying the distribution of stems provided additional insight relating to how spatial arrangement could affect each aquatic taxa, as opposed to a simple stem density estimate, which also ignores differences in stem sizes among vegetation taxa. For example, patches could have near identical stem densities but different VC scores based on how those stems are distributed among each quadrat. Open water patches provided a baseline of habitat use as those patches contain minimal structural complexity.

Age-0 bluegill and yellow perch were sampled within each habitat patch using cloverleaf traps (6.4 mm mesh, 50 cm lobes, and 12.7 mm lobe openings) for 3 consecutive days within each month to examine habitat use (see Kaemingk and Willis 2012 for more details). Juvenile bluegill and yellow perch are the most abundant fish in the littoral zone of Pelican Lake and often occupy emergent vegetation habitats during this life stage (Kaemingk and Willis 2012). Traps were checked twice daily every 12 h (i.e., daytime and nighttime), but only catches during daytime hours were used for this study so comparisons could be made across other aquatic taxa (i.e., zooplankton, benthic macroinvertebrates). Catch per unit effort (CPUE) was expressed as the mean number of age-0 fish captured per trap-hour.

Benthic macroinvertebrates and zooplankton were sampled once during the middle of each monthly fish sampling event (i.e., day 2 within a 3-day

Table 1. Site characteristics for the habitats sampled in Pelican Lake from August through October in 2009. Vegetation coverage was assessed by placing a 1 m² quadrat within each habitat type (VC score; similar to the Braun-Blanquet scale); 0–5% coverage = 1, 5–25% = 2, 25–50% = 3, 50–75% = 4, and 75–100% = 5 (Murry and Farrell 2007, Stahr et al. 2013). Mean (depth, Secchi disk transparency) and median (vegetation coverage) values are reported across habitat types, followed by ranges (minimum and maximum), except for open water and vegetation coverage (NA = not applicable).

<i>Habitat type</i>	<i>Depth (cm)</i>	<i>Secchi disk transparency (cm)</i>	<i>Vegetation coverage</i>
Cattail	76 (44-119)	24 (18-28)	5 (2-5)
Bulrush	89 (64-135)	24 (19-29)	2 (1-5)
Reed	79 (37-129)	24 (18-32)	3 (2-5)
Open water	147 (123-172)	23 (17-27)	NA

period) at each habitat patch. An Ekman grab sampler (231 cm²) was used to sample macroinvertebrates; samples were strained through a 583 µm mesh sieve in the field and stored in 90% ethanol. Macroinvertebrates were identified to order, except for the order Diptera, which was identified to family and enumerated using a dissecting microscope in the laboratory. Zooplankton samples were collected concurrently with benthic macroinvertebrate samples using a 2 m long tube sampler (Rabeni 1996). Zooplankton samples were filtered through a 65 µm mesh net in the field and stored in 90% ethanol. Three subsamples (diluted to a measured volume of 30 mL) were taken with a 5 mL Hensen-Stempel pipette and placed in a Ward counting wheel. Zooplankters (identified to genus for cladocerans and copepods) were enumerated within each subsample, and the total number of each taxon in a sample was calculated by dividing the number of organisms counted by the proportion of the sample volume processed. Density was calculated by multiplying the number of zooplankters of each taxon by the volume of the water filtered with the tube sampler. Taxon-specific length–dry-mass conversions were used to estimate biomass for both benthic macroinvertebrates (g/m²) and zooplankton (µg/L; Dumont et al. 1975, Smock 1980, Benke et al. 1999).

Data analysis

Age-0 yellow perch and bluegill habitat use in Pelican Lake was assessed using a repeated measures (sample site as the repeated measure and experimental unit, same site sampled during each month), 2-way analysis of variance (ANOVA) with habitat patch and month as the main effects (i.e., independent variable, including a 2-way interaction between these effects) on the relative abundance of each species (i.e., dependent variable). Mixed models were blocked by day (i.e., each sampling event averaged for each month) to account for variation in catch rates between sampling dates and further allow direct comparisons between the main effects included in each model. Differences in habitat use for macroinvertebrate and zooplankton taxa groups were each analyzed using a multivariate analysis of variance (MANOVA). This technique allowed broad community-level differences to be assessed while also taking into account specific taxon differences within macroinvertebrate and zooplankton groups. The Wilks' lambda was used to calculate the multivariate *F* statistic and associated *P* values. All statistical analyses were performed in R version 3.2.3 (R Development Core Team 2015) with an alpha of 0.10. Significant differences in either the ANOVA or MANOVA were further evaluated using a Tukey's HSD post hoc test. Some variables were log₁₀-transformed to better approximate normality and normalize residuals.

Results

A total of 18,007 age-0 bluegill and 1,434 age-0 yellow perch were sampled in Pelican Lake in 2009. Bluegills consistently used emergent vegetation more than open water ($F_{3,24} = 7.54, P < 0.01$; all Tukey's HSD: $P \leq 0.08$; Fig. 2) but no differences in habitat use were identified among emergent vegetation species. Bluegills were more abundant in September compared to August and October ($F_{2,24} = 20.56, P < 0.01$; all comparisons, Tukey's HSD: $P < 0.002$; Fig. 2). Yellow perch habitat use was greater within open water in August relative to the other emergent vegetation species (patch \times month interaction: $F_{6,24} = 2.79, P = 0.03$; Tukey's HSD: $P < 0.01$; Fig. 2). However, there were no differences in yellow perch abundance among habitat patches for both September and October (all comparisons, Tukey's HSD: $P > 0.10$; Fig. 2).

Benthic macroinvertebrate biomass varied across habitat patches ($F_{21,127} = 2.56, P < 0.01$) but remained similar across months ($F_{14,88} = 1.31, P = 0.22$).

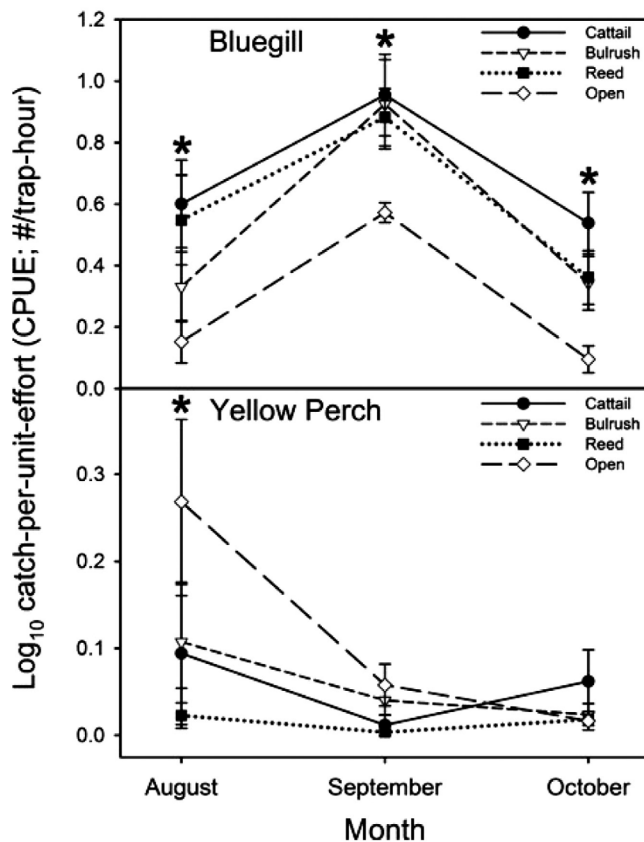


Figure 2. Log₁₀ catch-per-unit-effort (CPUE; #/trap-hour) of bluegill and yellow perch in Pelican Lake from August through October in 2009 within 4 habitat patches. An asterisk denotes a significant difference ($\alpha = 0.10$) between habitat patches within an individual month.

Invertebrate biomass was generally highest in cattails for many of the taxa sampled (Fig. 3). Gastropods were found in greater biomass in cattails than bulrush (Tukey's HSD: $P = 0.02$) and hirudinid biomass was greater in cattails than the other 3 habitat patches (all comparisons, Tukey's HSD: $P < 0.02$). Odonate biomass was higher in cattails than open water and reeds (all comparisons, Tukey's HSD: $P < 0.03$) but not bulrush (Tukey's HSD: $P = 0.26$). Amphipod biomass was higher in cattails (Tukey's HSD: $P = 0.01$) and bulrush (Tukey's HSD: $P = 0.26$) compared to open water. However, chironomid biomass was more abundant in open water compared to cattails (Tukey's HSD: $P = 0.05$).

Overall patterns of zooplankton biomass differed across patches and months (patch \times month interaction: $F_{42,182} = 1.46$, $P = 0.047$). However, these interaction patterns were not consistent (or significant) among all taxa (Fig. 4). For example, *Ceriodaphnia* biomass was greatest in open water compared to the vegetation habitat patches in September (all Tukey's HSD: $P < 0.01$). *Chydorus* biomass was higher in open water than cattail and reed (all comparisons, Tukey's HSD: $P < 0.05$) but no different than bulrush (Tukey's HSD, $P = 0.32$). Copepod nauplii biomass was greatest in open water compared to bulrush and cattails in September (Tukey's HSD: $P < 0.02$), but not compared to reeds (Tukey's HSD: $P = 0.99$).

Discussion

We found no major differences or consistent patterns across vegetation patches in overall habitat use for each taxonomic group. In general, the 3 emergent macrophytes in this study appear to function similarly for juvenile fishes, macroinvertebrates, and zooplankton. However, biomass of some macroinvertebrate taxa differed across emergent vegetation species whereas zooplankton biomass and juvenile fish abundance did not. Emergent macrophytes could serve a different role than open water habitat for fishes and zooplankton. For example, bluegill abundances were similar across vegetation types but higher in vegetation compared to adjacent open water habitats. While aquatic taxa could have migrated between patches, abundances should represent overall patch use (i.e., time spent in each habitat is related to the probability of being captured). These results suggest that emergent macrophytes may serve a similar ecological role across species yet still offer a distinct habitat for multiple trophic levels that is different from areas lacking aquatic vegetation.

One explanation for why we did not observe widespread differences across vegetation species is that structural complexity was comparable and thus habitats were not perceived differently across functional aquatic taxa. As noted previously, most of the complex growth for emergent macrophytes is

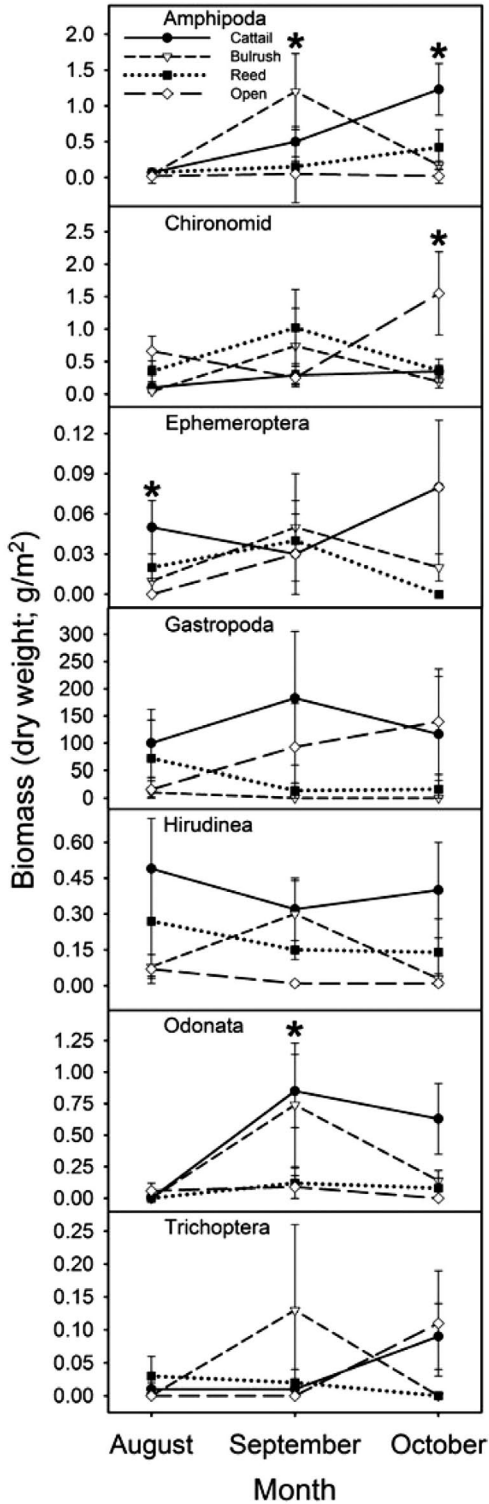


Figure 3. Biomass (dry weight; g/m²) of 7 benthic macroinvertebrate taxa in Pelican Lake from August through October in 2009 within 4 habitat patches. An asterisk denotes a significant difference ($\alpha = 0.10$) between habitat patches within an individual month.

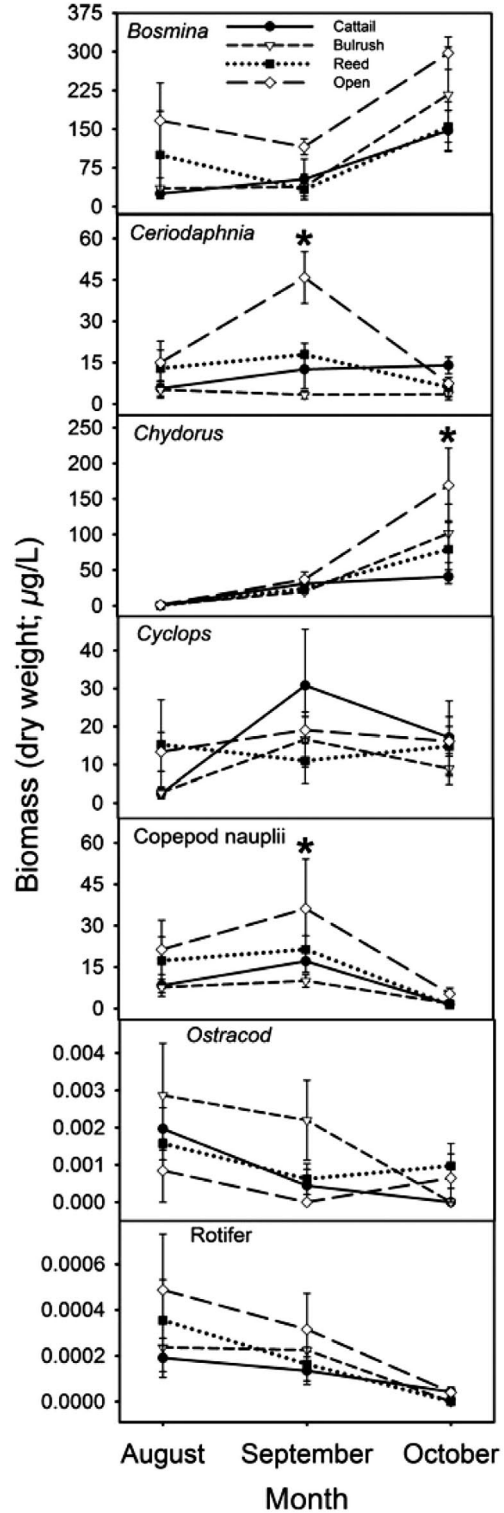


Figure 4. Biomass (dry weight; µg/L) of 7 zooplankton taxa in Pelican Lake from August through October in 2009 within 4 habitat patches. An asterisk denotes a significant difference ($\alpha = 0.10$) between habitat patches within an individual month.

inaccessible to aquatic organisms (e.g., predation refuge, foraging). Although some emergent macrophytes can have complex growth beneath the water's surface (e.g., American water willow [*Justicia americana*], swamp smartweed [*Polygonum hydropiperoides*]), the species in our study had relatively similar underwater growth forms. Increased structural complexity could also explain why submersed vegetation in these systems plays a larger role for supporting higher invertebrate densities and diversity compared to emergent macrophytes (Paukert and Willis 2003, Jolley et al. 2013). Other studies have also documented an increase in both macroinvertebrate taxa and density with greater aquatic macrophyte complexity (Thomaz et al. 2008). Chironomid abundances generally increased in Sandhill lakes with more emergent vegetation coverage, whereas submersed vegetation coverage was positively related to *Ceriodaphnia*, gastropod, and amphipod abundances (Paukert and Willis 2003). Size structure for some zooplankton was also related to submersed vegetation coverage, with larger sizes related to higher submersed macrophyte coverage (Paukert and Willis 2003). Collectively, differences in structural complexity between emergent and submersed vegetation may lead to contrasting responses from different trophic levels and divergent habitat use but not among emergent macrophyte species.

Another possibility that could explain the homogenous patterns observed among emergent vegetation species is the interaction between fish-predators and invertebrate-prey. Previous research in these Sandhill lakes did not show a strong fish predation influence on invertebrate abundances (Paukert and Willis 2003). That assessment, however, included all sizes of fish and was evaluated at a coarse spatial and temporal scale. Juvenile fishes typically search for and consume zooplankton and benthic invertebrates while avoiding predation (Werner et al. 1983). Invertebrates sampled in this study were consumed by both yellow perch and bluegill across August, September, and October in Pelican Lake (Kaemingk and Willis 2012). Both fish species have a history of competing for limited food resources across life stages in these systems (Kaemingk et al. 2012, Kaemingk et al. 2014). Age-0 yellow perch and bluegill demonstrated high diet overlap during the same time period investigated in this study, which appeared to compromise yellow perch growth rates due to high densities of age-0 bluegill (Kaemingk and Willis 2012). Therefore, competition for available food resources could restructure invertebrate abundances among habitat patches, ultimately influencing patterns in habitat use for juvenile fishes, zooplankton, and benthic macroinvertebrates.

Fishes often undergo shifts in habitat use during different life stages. Yellow perch were more abundant in open water habitat in August, but no differences existed between habitat patches in September or October. Yellow perch begin as pelagic larvae and then move into nearshore habitat

as juveniles (Post and McQueen 1988). This may explain why yellow perch were captured more in open water in August as they transitioned into the juvenile life stage. Bluegill also undergo ontogenetic habitat shifts similar to yellow perch, moving offshore initially after hatch to feed on zooplankton, then transitioning to nearshore habitats to escape predation (Werner and Hall 1988). However, we did not note this ontogenetic shift for bluegill in our study (i.e., vegetation was preferred across all months). This may be due to differences between submersed and emergent macrophytes or reflect the timing and duration of hatch between species (i.e., yellow perch hatch earlier and exhibit a shorter hatch duration than bluegill).

Benthic macroinvertebrates were the only trophic group that showed any divergent patterns among emergent vegetation species, suggesting that some taxa perceive and use these habitats uniquely. This pattern contrasts those observed for fish and zooplankton. For example, cattails contained higher biomass for a few benthic macroinvertebrate taxa. Some macroinvertebrates do specialize on certain macrophyte species (Dvřrak and Best 1982, Cyr and Downing 1988) and there may be characteristics inherent in cattails that serve as a better predation refuge (from fishes) than reeds and bulrush for invertebrates. Cattails have a different leaf form than bulrush and reed, as linear leaves originate from the base of the plant compared to bulrush (simple cylindrical stem) or reeds (linear leaves alternating on the stem but inaccessible below water; Larson 1993). Simple cylindrical stems can result in higher invertebrate capture rate by fishes compared to broader leaves (Dionne and Folt 1991). Thus, some invertebrates may prefer cattails due to the difference in growth form. However, future research should incorporate how structural complexity is perceived differently among aquatic taxa and how that difference may affect habitat use between macrophyte species.

Zooplankton also undergo shifts in habitat use, often migrating from open water during the night to structure during the day (Burks et al. 2002). Our results suggest that some zooplankton species may also use open water habitat during daytime hours and, in some cases, may be more abundant in these habitats compared to more structurally complex habitats. Zooplankton habitat use is complex and is determined by trade-offs related to interactions among predation risk (vertebrates and invertebrates), macrophyte composition and density, food quality and quantity, and abiotic factors such as light, temperature, and dissolved oxygen (Burks et al. 2002). In addition less is known about zooplankton habitat use in lakes dominated by emergent macrophytes, similar to our study system, that may lead to divergent patterns in horizontal migrations. Patterns in zooplankton biomass among habitat patches were not consistent across the months examined, further demonstrating this complexity and could be attributed to multiple dynamic biotic and abiotic processes.

Some zooplankton taxa were more abundant in open water habitats, despite no consistent pattern overall. For example, *Chydorus* are generally associated with open water habitats (Pennak 1989) and were observed in higher biomass within open water patches compared to the vegetated patches. This habitat use by *Chydorus* was further reflected in a previous study on Pelican Lake where *Chydorus* served as an important prey item for age-0 yellow perch and bluegill collected in open water habitats. This same study also found that age-0 yellow perch and bluegill consumed different zooplankton taxa within different habitat patches across the same months examined in this study (Kaemingk and Willis 2012). It also appears that, generally, both *Bosmina*–bluegill and *Chydorus*–yellow perch had near inverse patterns of habitat use among patches (Figs. 2 and 4). Bluegills were less abundant in open water habitat while *Bosmina* were most abundant in open water (although not statistically significant). Additionally, yellow perch were most abundant in open water habitat in August but had relatively equal habitat use among habitat patches in September and October. Conversely, *Chydorus* abundance was relatively equal among patches in August and September but significantly greater in open water habitat in October. These patterns could illustrate the complex relationship among predator and prey, whereby habitat use is either mediated by prey distribution (thus driving predator distribution) or by high risk of predation (thus driving prey distribution). Compared to submersed macrophytes, emergent macrophytes can provide increased foraging efficiency on zooplankton by sunfish (Dionne and Folt 1991). Our study adds to the existing literature stating that zooplankton can inhabit open water for predation refuge but also that zooplankton habitat use could either drive or be driven by predator distribution among habitat types.

Previous studies evaluating submersed macrophytes have found a trade-off between foraging efficiency and predation refuge for fishes as structural complexity increases (Werner and Hall 1988, Gotceitas 1990). For juvenile fishes, submersed macrophytes may be *too* complex depending on the plant species, thus making emergent macrophytes the preferred habitat, providing enough structural complexity to reduce predation risk but not restricting foraging (Stahr and Shoup 2015). However, for other aquatic taxa (such as invertebrates), higher macrophyte complexity may be consistently preferred due to increased food availability (e.g., algae colonization) *and* increased refuge from predation. Pelican Lake is unusual because the majority of macrophyte coverage is emergent vegetation instead of submersed vegetation (31% emergent coverage vs. 9.9% submersed coverage). In lakes and reservoirs with higher submersed macrophyte coverage (and higher species diversity of macrophytes), aquatic organisms could display a hierarchy in preferred habitat types (e.g., open water vs. emergent macrophytes

vs. submersed macrophytes vs. floating-leaved macrophytes) depending on the imperative need of structural complexity by the organism (e.g., foraging, predation refuge, intra- and interspecific competition). These habitat preferences or requirements may also change across developmental stages and seasons. Future studies should focus on testing this hypothesis among habitat types and whether habitat use may change depending on the functional role of each organism.

Due to the importance of macrophytes to lentic environments, managers often invest considerable resources to maintain macrophyte coverage in lakes and reservoirs. However, establishing macrophytes in lakes can be challenging and managers are often forced to identify plants that can grow in difficult environmental conditions (Collingsworth et al. 2009). Emergent macrophytes are often used in lakes for both limnologic goals (stabilizing sediment, reducing wind and wave action) and providing habitat to aquatic organisms (such as juvenile fishes). From a physical structure aspect, our results suggest that, in lakes lacking vegetation coverage, managers may be able to choose from a variety of emergent macrophyte species without comprising ecological trade-offs. But, there are likely other species-specific characteristics that managers should take into account when introducing species (e.g., root structure). Managers also need to weigh the cost and benefit of emergent vegetation introductions as these species, like all aquatic vegetation types, can grow to nuisance levels in lentic ecosystems (e.g., Galatowitsch et al. 1999). By recognizing functional responses to macrophytes across trophic levels, managers may be able to focus more strategically on achieving certain social goals while still addressing ecological objectives (such as predation refuge and food availability). Although this study was conducted within a single year on a single lake, it is the first to directly investigate use of multiple aquatic taxa groups among multiple emergent macrophyte species. Future research should focus on understanding how the patterns of habitat use in our study compare to other lentic ecosystems with respect to emergent macrophyte species and individual lake characteristics.

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