

**Ecological effects of water hyacinth (*Eichhornia crassipes*) on Lake Chapala, Mexico**

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## ABSTRACT

Water hyacinth (*Eichhornia crassipes*) is a floating non-native plant that has been reoccurring in Lake Chapala, Jalisco, Mexico for more than 100 years. In this research, I explore the effects of water hyacinth on freshwater ecosystems worldwide and specifically on Lake Chapala.

In chapter 1, I reviewed studies conducted on water hyacinth worldwide and found that the effects of water hyacinth on water quality are similar but the magnitude of effects is dependent on the percent cover and potentially the spatial configuration of water hyacinth mats. Water hyacinth's effect on aquatic invertebrates, fish, and waterbirds is less predictable and dependent on conditions prior to invasion. In chapter 2, I tested for relationships between percent water hyacinth cover and waterbird abundance, species diversity, community composition, and habitat use. In general, I found a weak positive relationship or no relationship between these variables. In Chapter 3, I monitored habitat use by American Coots (*Fulica americana*) in a variety of habitats around Lake Chapala. I found that the time spent in water hyacinth positively corresponded to the percent water hyacinth cover and that the time foraging in water hyacinth was positively related to the time spent in water hyacinth.

In Chapter 4, I compared invertebrate assemblages in open water to those within and at the edge of water hyacinth mats, emergent vegetation, and submerged trees. I also examined invertebrate assemblages within the roots of water hyacinth plants and compared assemblages

between patch and shoreline water hyacinth plants. I found that density and taxonomic richness of water column invertebrates were generally higher in association with water hyacinth, but that mean percent cover of water hyacinth affected the magnitude of differences among habitats and vegetation types. I did not find significant differences in root invertebrate density and taxonomic richness between patch and shoreline water hyacinth plants. In chapter 5, I discuss how water hyacinth affected dissolved oxygen and water transparency on a small, localized scale, but was not the driving factor for seasonal differences. The overall results suggest that water hyacinth had a minimal ecological effect on Lake Chapala during this study.

## **Dedication**

I dedicate this dissertation to my grandmother, Margaret Hagen, who passed earlier this year. Her strength of character and perseverance has guided me through my life. Oma, I wish you could be here to share in this achievement.

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This dissertation is a product of years of support and encouragement. I want to thank David Trauger for meeting with me one random Friday and convincing me to transfer to Virginia Tech from Hawaii. A special thanks to Brian Murphy for taking me in as a student of his own, getting me involved with Lake Chapala and the Universidad Autónoma de Guadalajara (UAG), and for sharing in the eternal curiosity that drives learning. José Luis Zavala (UAG) has helped tremendously with on-the-ground logistics and provided valuable advice on field work and experimental design, not to mention suggestions for the best tacos, micheladas, and carne en su jugo. I also want to thank Sarah Karpanty for playing a huge role on my committee, serving as a co-advisor for my *AdvanceVT* fellowship, and sharing in a commitment to using case studies in the classroom. A number of students/friends have volunteered their time in the field to collect zooplankton samples, measure dissolved oxygen and Secchi depth, and participate in this adventure: Brad Ray, Maggie Peirce, Shane Mitchell, and Eric Ferryman. Additional thanks to Rebecca Rossmair, Maggie Peirce, Stephen Via, and Erica Nicholson for their incredible help and organization in the lab. I couldn't ask for better. I also would like to acknowledge my family and friends for their endless love, support, and sense of humor. I can't imagine this crazy road without you. Support for this research came from several sources: the College of Natural Resources (VT), an NSF Advance grant (#SBE-0244916), the Acorn Alcinda Foundation of Lewes, Delaware, the Waste Policy Institute (WPI), and the Virginia Lakes and Watershed Association.

## Foreword

This dissertation is formatted as 6 publishable manuscripts (Chapters 1-6). Tables and figures are repeated among chapters and formatting differences (e.g. section headings, literature cited, table, and figure formats) exist due to journal specific requirements. The first chapter is a comprehensive literature review of the ecological and socio-economic effects of water hyacinth worldwide. It is currently under review with the *Freshwater Biology* journal. The second chapter is formatted for submission to the *Waterbirds* journal, the third to the *Journal of Field Ornithology*, and the fourth and fifth chapters are formatted for *Hydrobiologia*. The sixth chapter provides a synthesis of the first 5 chapters and it is formatted for the *Freshwater Biology* journal.

## Attribution

Brian R. Murphy is a co-author on chapter 1 that is currently in review with the *Freshwater Biology* journal. Brian's contribution to this manuscript included preliminary literature review planning and editing the manuscript for publication.

Brian R. Murphy and José Luis Zavala will be listed as co-authors on chapter 4 when submitting to *Hydrobiologia*. Brian's contribution to this manuscript included project planning and editorial review. José Luis' contribution to this manuscript included experimental design and statistical advice as well as logistical field support in Mexico.

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## Chapter 1

### Ecological and socio-economic effects of water hyacinth (*Eichhornia crassipes*): a review\*

\*In review as:

Villamagna, A.M. and B.R. Murphy. 2009. Ecological and socio-economic effects of water hyacinth (*Eichhornia crassipes*): a review. *Freshwater Biology*

#### Summary

1. Water hyacinth (*Eichhornia crassipes*) is one of the world's most prevalent invasive aquatic plants and is known to cause significant ecological and socio-economic change.
2. Water hyacinth can change water quality by altering water clarity and decreasing phytoplankton production, dissolved oxygen, nitrogen, phosphorous, heavy metals, and other contaminant concentrations.
3. Water hyacinth has mixed effects on zooplankton abundance and diversity. Zooplankton abundance tends to decrease in response to decreased phytoplankton availability, but populations may increase in response to increased refuge from predators.
4. Macroinvertebrate abundance and diversity generally increase in response to increased habitat heterogeneity and structural complexity provided by water hyacinth.
5. Effects of water hyacinth on fish are largely dependent on original community composition and food-web structure. A more diverse and abundant epiphytic invertebrate community may increase fish abundance and diversity, but the loss of phytoplankton may decrease the abundance of certain planktivorous fish species which can subsequently affect higher trophic levels.

6. Little is known about the effects of water hyacinth on waterbird communities; however, increases in macroinvertebrate and fish abundance and diversity suggest a potentially positive interaction with waterbirds when water hyacinth is at moderate density.
7. The socio-economic effects of water hyacinth are dependent on the extent of the invasion, the uses of the impacted water body, control methods, and the response to control efforts.
8. Ecosystem-level research programmes that simultaneously monitor the effects of water hyacinth on multiple trophic-levels are needed to further our understanding of invasive species.

**Keywords** Water hyacinth, *Eichhornia crassipes*, Water quality, Invertebrates, Fish, Waterbirds, Socio-economic

## **Introduction**

Originally from South America, water hyacinth, *Eichhornia crassipes* (Mart.) Solms, is one of the world's most prevalent invasive aquatic plants. Water hyacinth, a floating vascular plant, is known to cause major ecological and socio-economic changes (Center, 1994). It commonly forms dense, interlocking mats due to its rapid reproductive rate and complex root structure (Mitchell, 1985). Water hyacinth reproduces both sexually and asexually. Ten to 100% of existing seeds are found to germinate within six months, with dry conditions promoting germination (Ueki & Oki, 1979). Nutrients and temperature are considered the strongest determinants for water hyacinth growth and reproduction (Wilson *et al.* 2007). Salinity constraints generally limit water hyacinth establishment in coastal areas and within estuaries (Mangas-Ramirez & Elias-Gutierrez, 2004). Low temperatures and winter ice cover currently

limit water hyacinth from spreading into cooler latitudes (Rodríguez-Gallego *et al.*, 2004); however, recent climate change models suggest that the distribution of aquatic invasive species is likely to expand in temperate regions (Hellmann *et al.*, 2008; Rahel & Olden, 2008).

Water hyacinth has invaded freshwater systems in over 50 countries on five continents; it is especially pervasive throughout Southeast Asia, the southeastern United States, central and western Africa, and Central America (Bartodziej & Weymouth, 1995; Brendonck *et al.*, 2003; Lu *et al.*, 2007; Martinez Jimenez & Gomez Balandra, 2007). It is prevalent in tropical and subtropical water bodies where nutrient levels are often high due to agricultural runoff, deforestation, and insufficient wastewater treatment. There is not a clear record of how, why, and when water hyacinth was introduced to water bodies outside of its native range, but many populations are well established and persistent despite control efforts. Its success as an invader is attributed to its ability to outcompete native vegetation and phytoplankton for light and its release from consumers (*Neochetina eichhorniae* and *N. bruchi*) found within its native range (Wilson *et al.* 2007). Invasions vary in extent and duration but generally cause similar problems. Changes to water hyacinth density have the potential to affect other ecological and human communities in areas where it is established; these changes may be perceived as positive or negative depending on the designated or beneficial uses of the waterbody (Gibbons *et al.*, 1994).

Water hyacinth is extremely difficult to eradicate once established. Therefore, the goal of most management efforts is to minimize economic costs and ecological change. Recent literature on the management of water hyacinth focuses on techniques to remove the weed; however, little has been done to assess the full extent of ecological changes (i.e. abiotic and biotic) that may occur in response to the establishment and management of this non-native species. Determining the consequences of controlling an established water hyacinth population

is contingent on our ability to understand how water hyacinth affects the systems that it inhabits. There are very few studies that report the ecological conditions prior to invasion. This makes it difficult to understand fully how water hyacinth alters an ecosystem. We rely on scientific accounts that either compare water quality and ecological condition between sites with and without water hyacinth or examine the changes that occur after a control programme is implemented. Many investigations focus on one element of an ecosystem at a time (e.g. nutrient concentration, dissolved oxygen, plant or animal community composition); however, it is necessary to look at effects on the system as a whole to comprehend the direct and indirect impacts of this aquatic plant.

The objectives of this paper are two-fold. First, we provide a concise review of publications from the last 30 years that examine the effects of water hyacinth on water quality, the community composition of zooplankton, macroinvertebrates, fish, and birds, and socioeconomic condition. We discuss the dominant control programmes and ecological consequences, and provide several cases as examples. The literature on water hyacinth is extensive, but accessibility can be challenging. By synthesizing the results of these studies, we hope to enhance managers' access to global scientific information and their understanding of water hyacinth as an invasive species. Second, we identify gaps in current scientific understanding and offer suggestions for future research that will promote stronger understanding of water hyacinth dynamics and aid in the management of this invasive species.

## Effects of water hyacinth on water quality

Prior research on water hyacinth's effects on water quality has focused mainly on the consequences of the dense mats formed by the interlocking of individual plants. The most commonly documented effects are lower phytoplankton productivity and dissolved oxygen concentrations beneath mats (Rommens *et al.*, 2003; Mangas-Ramirez & Elias-Gutierrez, 2004; Perna & Burrows, 2005). Other water quality effects include higher sedimentation rates within the plant's complex root structure and higher evapotranspiration rates from water hyacinth leaves when compared to evaporation rates from open water (Gopal, 1987). Water hyacinth also has been found to stabilize pH levels and temperature in experimental lagoons, thereby preventing stratification and increasing mixing within the water column (Giraldo & Garzon, 2002). Photosynthesis is limited beneath water hyacinth mats, and the plant itself does not release oxygen into the water as do phytoplankton and submerged vegetation (Meerhoff *et al.*, 2003), resulting in decreased dissolved oxygen concentration. The extent of dissolved oxygen reduction is dependent on the capacity of the water hyacinth mat to prevent light infiltration into the water column. Water hyacinth was associated with significantly lower concentrations of dissolved oxygen when compared to *Hydrilla verticillata* and *Sagittaria lancifolia* L. (Troutman *et al.*, 2007). Similarly, water hyacinth had lower dissolved oxygen concentrations when compared to *Myriophyllum spicatum*, *H. verticillata*, and *Potamogeton spp.*, and it was the only plant associated with average dissolved oxygen concentrations less than 5 mg L<sup>-1</sup> (Toft *et al.*, 2003). Masifwa *et al.* (2001) found an inverse relationship between dissolved oxygen concentrations beneath water hyacinth mats and the distance to open water. The percent cover, or mat size, of water hyacinth that causes notable decreases in dissolved oxygen is not known but likely varies with the system. McVea and Boyd (1975) found that up to 25% cover of 0.04-ha experimental

ponds did not cause dissolved oxygen to reach levels that threaten fish survival (less than 2mg l<sup>-1</sup>), although they did find an inverse negative relationship between dissolved oxygen and water hyacinth cover.

Water hyacinth also absorbs heavy metals (Tiwari *et al.*, 2007), organic contaminants (Zimmels *et al.*, 2007), and nutrients from the water column (Aoi & Hayashi, 1996). In California, water hyacinth leaf tissue was found to have the same mercury concentration as the sediment beneath, suggesting that plant harvesting could help mediate mercury contamination if disposed of properly (Greenfield *et al.*, 2007). On a similar note, water hyacinth's capacity to absorb nutrients makes it a potential biological alternative to secondary and tertiary treatment for wastewater (Ho, 1994; Cossu *et al.*, 2001).

In a laboratory-based experiment designed to mimic nutrient conditions of Lake Chivero, Uganda, Rommens *et al.* (2003) tested water hyacinth's uptake capacity to absorb nitrate (NO<sub>3</sub>), ammonium (NH<sub>4</sub>), and phosphate (PO<sub>4</sub>) from the water column. The average water hyacinth plant absorbed 2.36 mg of ammonium, 1.13 mg of nitrate, and 0.39 mg of phosphate per kilogram of water hyacinth (wet weight) each hour. From a management perspective, these results could be used to estimate potential nutrient response in systems where water hyacinth has been introduced or where it has been removed.

Water hyacinth's uptake capacity has been validated in several field studies as well. It has a high nutrient uptake rate compared to other macrophytes (Rodríguez-Gallego *et al.*, 2004); therefore, it has the potential to significantly reduce nutrient concentrations in a water body depending on the extent of cover and density (Pinto-Coelho & Greco, 1999). Overall, nutrient uptake is thought to vary by season, with greater uptake in the summer when temperatures are

higher and more favorable for plant growth (Rommens *et al.*, 2003; Rodríguez-Gallego *et al.*, 2004). Rommens *et al.* (2003) found that littoral sites with water hyacinth in Lake Chivero, Zimbabwe, had significantly less ammonium, nitrate, and dissolved oxygen ( $\text{mg l}^{-1}$ ) than limnetic sites or than littoral sites without water hyacinth; however, chlorophyll-a concentrations were higher in sites with water hyacinth. This may have been attributed to the ability of water hyacinth to trap existing phytoplankton and detritus, but it is unlikely that chlorophyll-a concentrations would remain high as water hyacinth density increased and light penetration decreased. Greenfield *et al.* (2007) found significantly higher total nitrogen and phosphorus in the water column following the shredding of water hyacinth. Similarly, Marshall (1997) noted an increase in nitrogen and phosphorus after water hyacinth was controlled biologically in Lake Chivero during the 1990s; prior to control, water hyacinth covered 30% of the lake. Although there is potential for water hyacinth to provide phytoremediation in highly eutrophic systems (Rodríguez-Gallego *et al.*, 2004), the nutrient reductions would depend on the density of water hyacinth cover. Therefore, the net benefits of a phytoremediation approach would also depend on other impacts by water hyacinth. As previously discussed, biological respiration increases with increasing plant density and could lead to anaerobic conditions beneath water hyacinth mats. Moreover, upon senescence plants release nutrients back into the water column (Rodríguez-Gallego *et al.*, 2004), thereby negating the benefits of nutrient removal from highly eutrophic systems (Giraldo & Garzon, 2002). Table 1 provides a summary of the reports that focused on water quality impacts.

**Table 1: A summary of 19 studies that focused on the effects of water hyacinth (*Eichhornia crassipes*) on dissolved oxygen concentrations, nutrient concentrations, phytoplankton density (chlorophyll-a concentrations), heavy metals, and other contaminants. Downward arrows represent a decrease in the parameter with an increase in water hyacinth; upward arrows represent an increase in the parameter with an increase in water hyacinth cover. All studies were conducted outside of water hyacinth's native range.**

Author	Location	Dissolved Oxygen	Nutrients	Phytoplankton	Water Quality (misc)	Contaminants
Rommens <i>et al.</i> , (2003)	Lake Chivero, Zimbabwe	↓	↓	↑	↑ transparency	
Mangas-Ramirez & Elias-Gutierrez (2004)	Valsequillo Reservoir, Mexico	↓		↓		
Perna & Burrows, (2005)	Burdekin River, Australia	↓				
Gopal, (1987)	General review				↑ Evaporation Sedimentation	
Giraldo & Garzon, (2002)	Bogota River (reservoir), Colombia				Stabilized Temperature & pH	
Meerhoff <i>et al.</i> , (2003)	Lake Rodó, Uruguay	↓				
Troutman <i>et al.</i> , (2007)	Atchafalaya River, Louisiana	↓				
Toft <i>et al.</i> , (2003)	Sacramento-San Joaquin River, California	↓				
Masifwa <i>et al.</i> , (2001)	Lake Victoria, Uganda	↓				

**Table 1 continued**

Author	Location	Dissolved Oxygen	Nutrients	Phytoplankton	Water Quality (misc)	Contaminants
McVea & Boyd, (1975)	Experimental ponds	↓				
Tiwari <i>et al.</i> , (2007)	Shahpura Lake, Bhopal					↓
Greenfield <i>et al.</i> , (2007)	Sacramento-San Joaquin River, California		↓	↓		↓
Ho, (1994)	Wastewater treatment plant					↓
Cossu <i>et al.</i> , (2001)	Laboratory – Municipal waste					↓
Aoi & Hayashi, (1996)	Outdoor batch culture system experiment		↓	↓		
Zimmels <i>et al.</i> , (2007)	Laboratory – Waste water					↓
Rodríguez-Gallego <i>et al.</i> , (2004)	Lake Rodó, Uruguay	↓				
Pinto-Coelho & Greco, (1999)	Pampulha Reservoir, Brazil (native)	↓				
Marshall, (1997)	Lake Chivero, Zimbabwe		↓	↓		

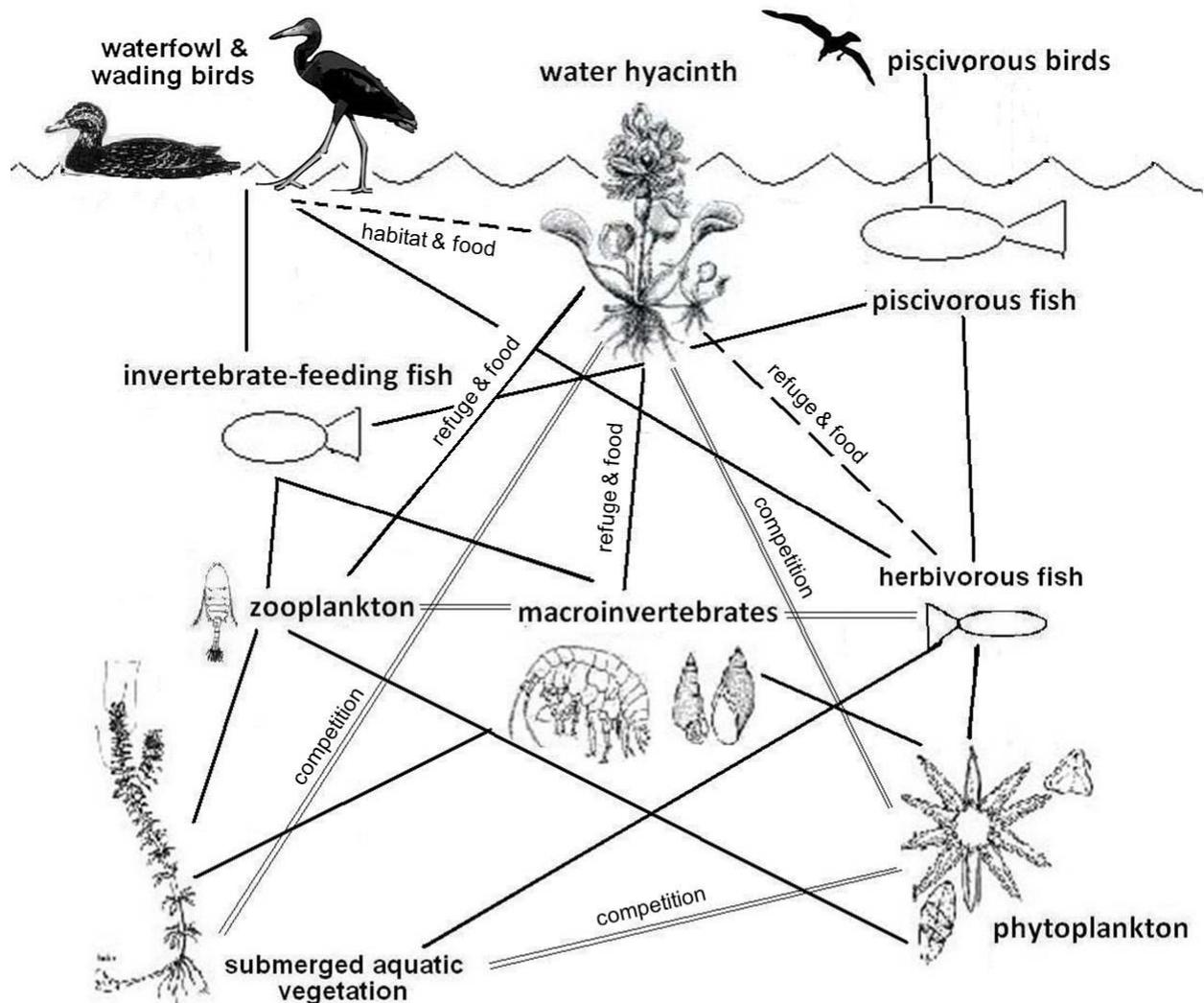
## **Effect of water hyacinth on ecological communities**

The structure of a macrophyte assemblage plays a large role in determining composition of phytoplankton, zooplankton, fish, and birds in freshwater ecosystems (Murkin & Kadlec, 1986; Meerhoff *et al.*, 2006), as illustrated in Figure 1 below. As a floating plant, water hyacinth offers unique and complex structure to the freshwater ecosystems in which it establishes (Arora & Mehra, 2003). A shift in the primary-production base of a lake can resonate throughout the ecosystem, affecting multiple trophic levels both directly through changes in habitat availability and indirectly through shifts in energy pathways. The strong interdependence among biological communities within aquatic ecosystems makes it difficult to predict the impacts of a non-native species without understanding fully the existing system and the effects of that non-native on various components of the ecosystem. In the subsections to follow, we examine the ecological effects of water hyacinth on specific components of lake ecosystems.

### ***Phytoplankton and Macrophytes***

Water hyacinth often establishes in areas that lack significant aquatic vegetation, but it is also able to out-compete submersed vegetation and phytoplankton (Mitchell, 1985). Free-floating plants are able to monopolize light and absorb nutrients from the water column, preventing phytoplankton and submersed vegetation from obtaining sufficient resources for photosynthesis (McVea & Boyd, 1975). Therefore, free-floating plants can dominate phytoplankton and submerged vegetation when natural controls do not exist outside of native range (Scheffer *et al.*, 1993; Roijackers *et al.*, 2004). Water hyacinth was found to selectively

**Figure 1: Interactions within an ecosystem with an established non-native water hyacinth (*Eichhornia crassipes*) population. Lines represent verified relationships between ecological components (i.e. energy flow and habitat use). Dashed lines represent potential relationships that have yet to be documented.**



inhibit planktonic green algae in a shallow Portuguese lake (Almeida *et al.*, 2006), yet phytoplankton density in littoral sites with water hyacinth in Lake Chivero, Uganda was 10-30 times higher than littoral sites without water hyacinth (Brendonck *et al.*, 2003). Water hyacinth can entrap phytoplankton and detritus thereby increasing, at least temporarily, phytoplankton

densities beneath mats (Brendonck *et al.*, 2003). Following the removal of water hyacinth in its native range, Bicudo *et al.* (2007) found a substantial increase in total phytoplankton as well as cyanobacteria biomass that contributed to the loss of water clarity in a shallow Brazilian reservoir. Similar results were found in two Mexican reservoirs where phytoplankton and cyanobacteria increased after removal of water hyacinth (Lugo *et al.*, 1998; Mangas-Ramirez & Elias-Gutierrez, 2004). Overall, water hyacinth seems to limit the productivity of phytoplankton and submersed vegetation under mats, with the exception of certain colonial types that may initially be captured within water hyacinth roots. The literature also suggests at least a temporary shift toward cyanobacteria following removal of water hyacinth.

### ***Zooplankton***

Zooplankton distribution can be influenced by turbulence, light intensity, temperature, chlorophyll-a, dissolved oxygen (Kiorboe & Saiz, 1995), and food availability (Richards *et al.*, 1985; Maccina *et al.*, 1992). Changes to zooplankton community diversity and abundance are commonly linked to a shift in the macrophyte community via changes to habitat (Richards *et al.*, 1985), but they are also attributed to changes in the density and community composition of zooplankton predators (Meerhoff *et al.*, 2003). Reduced phytoplankton productivity can decrease zooplankton abundance by decreasing food availability (Richards *et al.*, 1985; Maccina *et al.*, 1992). On the other hand, the complex structure provided by macrophytes may provide more microhabitats for epiphytic zooplankton. This was documented in Egypt where there was a more abundant and diverse epiphytic rotifer community within water hyacinth than within *Salvinia molesta*, a macrophyte with smaller floating and submerged leaves. The difference in

rotifer abundance and species richness was attributed to greater food availability and refuge from predators provided by water hyacinth's complex root structures (Arora & Mehra, 2003).

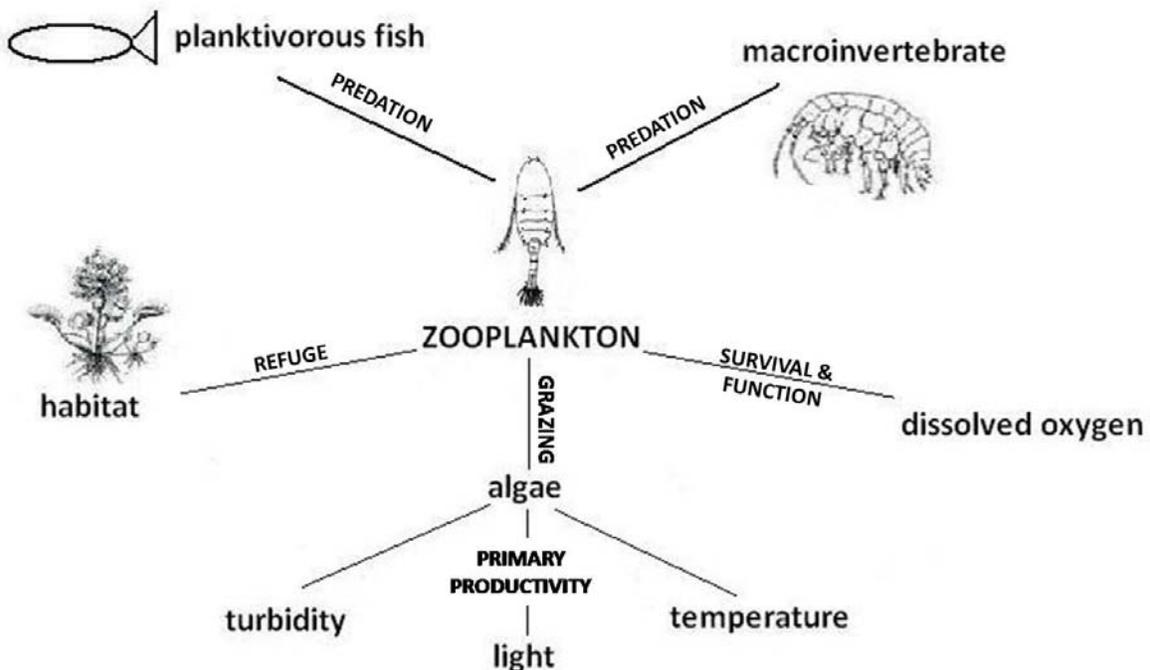
Overall, zooplankton response to water hyacinth appears to vary by taxa and geographic location. Meerhoff *et al.* (2003) did not find a significant difference in microcrustacea richness or diversity among sites with water hyacinth, sites with pondweed (*Potamogeton pectinatus*), or vegetation-free littoral sites of Lake Rodo, Uruguay. Cladoceran abundance did not differ among sites, but calanoid and cyclopoid copepods were less abundant in sites with water hyacinth than sites with *P. pectinatus* or vegetation-free littoral sites (Meerhoff *et al.*, 2003). Total rotifer abundance was highest in open water, but differed little among other microhabitats. In contrast, a decrease in calanoid copepods was recorded after a mechanical water hyacinth control programme was initiated in a Mexican reservoir. Cyclopoid copepod and cladoceran abundance did not change after water hyacinth was removed, but cladoceran species composition shifted (Mangas-Ramirez & Elias-Gutierrez, 2004). In yet another study, microcrustacean taxa were more abundant at littoral sites without water hyacinth than littoral sites with water hyacinth (Brendonck *et al.*, 2003).

The variation in water hyacinth's effects on zooplankton (Table 2) suggests that there are other factors contributing to the zooplankton response. Among these factors could be algal concentrations and physiochemical conditions at the time of sampling, the time of day at which zooplankton was sampled, the presence of predators and the effects of water hyacinth on potential predators, and the spatial configuration of water hyacinth (Figure 2). Zooplankton migrate throughout an ecosystem, both vertically and horizontally (Roijackers *et al.*, 2004; Iglesias *et al.*, 2007; Meerhoff *et al.*, 2007); therefore, it is important to incorporate the time of day into any analysis of habitat use. Moreover, zooplankton may be affected by water hyacinth

**Table 2: Results from 4 studies that focused on the effects of water hyacinth (*Eichhornia crassipes*) on the zooplankton community.**

Author	Location	Differences between sites with and without water hyacinth
Meerhoff <i>et al.</i> (2003)	Lake Rodo, Uruguay	Copepoda was less abundant at sites with water hyacinth  No difference in microcrustacea between sites Rotifera was highest in open water at sites without water hyacinth
Arora and Mehra (2003)	Yamuna River, India	More abundant and diverse epiphytic rotifer groups
Mangas-Ramirez and Elias-Gutierrez (2004)	Valsequillo Reservoir, Mexico	Cladocera species composition differs within sites with water hyacinth  No difference in cladoceran or cyclopoid copepod abundance between sites
Brendonck <i>et al.</i> (2003)	Lake Chivero, Uganda	More abundant microcrustacea in sites without water hyacinth

**Figure 2: Various factors affecting zooplankton community composition and abundance.**



differently outside of its native range. Meerhoff *et al.* (2007) found that horizontal diel movements were more pronounced in temperate than subtropical water bodies, even though vertical movements were similar. Greater horizontal movement may allow temperate zooplankton to move in and out of water hyacinth mats to a greater extent than tropical zooplankton, thus avoiding some of the detrimental effects (e.g. low dissolved oxygen and lack of phytoplankton) under large mats.

### ***Macroinvertebrates***

Aquatic plants provide ideal habitat for larger macroinvertebrate colonization as well (Sharitz & Batzer, 1999; Masifwa *et al.*, 2001b). Structure provided by the roots and leaves create complex habitat for macroinvertebrates, especially for epiphytic macroinvertebrates like snails, arachnids (Brendonck *et al.*, 2003), and amphipods (Toft *et al.*, 2003; Rocha-Ramirez *et al.*, 2007). Several studies have documented a positive correlation between epiphytic macroinvertebrate densities and the surface area of floating aquatic vegetation, including water hyacinth (Crowder *et al.*, 1982; Schramm *et al.*, 1987). Within its native range, water hyacinth is an important substrate for invertebrate colonization (de Marco *et al.*, 2001). Macroinvertebrate densities tend to be higher near the open water edge of water hyacinth mats compared to the center. For example, the largest quantities of macroinvertebrates sampled from water hyacinth in swamps along the Nile River were found within 6 m of open water (Bailey & Litterick, 1993).

O'Hara (1967) examined macroinvertebrates within the roots of water hyacinth introduced to Lake Okeechobee, Florida. He found that the macroinvertebrates were typical benthic species in the same area, but macroinvertebrate abundance within the roots of water

hyacinth was greater than in benthic samples or within other plant-root systems. No correlation was found between macroinvertebrate abundance and root mass. Table 3 provides a list of the dominant macroinvertebrates identified in conjunction with water hyacinth, but O'Hara (1967) also identified macroinvertebrates from the classes Oligochaeta, Turbellaria, Hirudinidea, Pelecypoda, Arachnida, Insecta, and the subphylum of Crustacea. Rocha-Ramirez (2007) also found a highly diverse macroinvertebrate assemblage (96 taxa) within water hyacinth roots in a coastal lagoon of Mexico and species composition of Ephemeroptera shifted during periods of high and low salinity. This study suggested that assemblage composition was not only affected by the presence of water hyacinth, but also by physiochemical conditions such as salinity, dissolved oxygen, and turbidity. De Marco *et al.* (2001) found that invertebrate assemblages associated with water hyacinth within its native range were dominated by detritivores, mainly Oligochaeta, Turbellaria, and a non-native gastropod. The authors attributed this dominance to detritus retention within the roots. They also found a positive correlation between the density of some invertebrates and dissolved oxygen within the water hyacinth roots. Overall, there are few differences reported in the invertebrate communities associated with water hyacinth roots between sites within and outside the plant's native range (Table 3).

Macroinvertebrates are generally more abundant in association with aquatic macrophytes than in open water (Mitchell & Marshall, 1974; Olson *et al.*, 1994). In Lake Victoria, Uganda, floating macrophytes, including water hyacinth, at the open-water interface supported more macroinvertebrates and a richer assemblage compared to the rooted emergent vegetation. These floating macrophyte species harbored more macroinvertebrates than open water (Masifwa *et al.*, 2001a). When macroinvertebrate assemblage was compared in the Sacramento-San Joaquin Delta between water hyacinth and pennywort, a native floating macrophyte, Toft *et al.* (2003)

found the two macrophytes supported different macroinvertebrate assemblages. Results from a study on Lake Chapala, Mexico, also suggest richer and more-abundant macroinvertebrate communities within the roots of water hyacinth than found in open water or within emergent vegetation stand (Villamagna, 2009).

**Table 3: The most abundant invertebrate groups identified in five studies of water hyacinth (*Eichhornia crassipes*).**

Author	Location	Most abundant invertebrates
O'Hara (1967)	Lake Okeechobee, USA (FL)	Gastropoda and insect larvae
Bailey and Litterick (1993)	Nile River, Sudan	Gastropoda and Coleoptera
Masifwa <i>et al.</i> (2001)	Lake Victoria, Uganda	Gastropoda, Chironomidae, Ephemeroptera, and Hirundinea
Rocha-Ramirez <i>et al.</i> (2007)	Alvarado Lagoonal System, Mexico	Isopoda and Ephemeroptera
de Marco <i>et al.</i> (2001)	Pampulha Reservoir, Brazil (native range)	Oligochaeta and Turbellaria

Researchers in Florida took an experimental approach to determine the effects of water hyacinth mats on the macroinvertebrate and fish communities associated with native submerged vegetation *Sagittaria kurziana*. Epiphytic macroinvertebrate abundance within the submerged vegetation initially decreased with the addition of a water hyacinth canopy, but total macroinvertebrate abundance did not differ. Total macroinvertebrate abundance within sites with water hyacinth and *S. kurziana* was significantly greater than sites without water hyacinth during the fall and winter, starting approximately 80 days after the introduction of water

hyacinth. Taxa richness was consistently greater at sites with water hyacinth and *S. kurziana* and assemblages differed between the plants as well (Bartodziej & Leslie, 1998). Together these studies support the conclusion that water hyacinth can enhance macroinvertebrate abundance and richness through the provision of additional, and in some cases novel, habitat. An increase in abundance and diversity of macroinvertebrates could subsequently affect food web structure with potential consequences for fish and birds, to be discussed in the following sections.

### ***Fish***

The effects of water hyacinth on fish communities depend on the initial community composition and structure, the existing food web, and likely water hyacinth density or area cover. Fish density and species composition are known to vary across macrophyte habitats with different levels of food availability, plant density, structural complexity, and physiochemical factors (Grenouillet *et al.*, 2002; Lewin *et al.*, 2004). Grenouillet *et al.* (2002) found fish abundance and species richness to increase with food availability and to be highest in habitats with intermediate structural complexity. Similar results were reported by Meerhoff *et al.* (2003) where fish abundance was highest in submerged vegetation, followed by water hyacinth and vegetation-free littoral sites. The removal of submerged vegetation in this system increased use of water hyacinth and vegetation-free littoral sites by the most common fish species. Although total fish biomass did not differ between water hyacinth and *Hydrilla verticillata* in Louisiana, differences in species composition were detected (Troutman *et al.*, 2007). Compared to submerged or emergent vegetation, water hyacinth provides a highly complex structure near the surface of the water, and it acts similar to a forest canopy by restricting vegetative growth below.

This modification of architecture at the surface of the water adds structural complexity and heterogeneity that likely affects macroinvertebrates and fish (Meerhoff *et al.*, 2006; Meerhoff *et al.*, 2007).

Water hyacinth can change fish diets through changes in prey availability. Toft *et al.* (2003) found that the macroinvertebrates associated with water hyacinth were not the same species as the common prey of fish captured near the edge of water hyacinth mats. This could result in a dietary shift to include more abundant species of macroinvertebrates that occur as a result of water hyacinth. A similar situation occurred in Lake Victoria where Nile perch (*Lates niloticus*) shifted their diets to include a larger component of insects specifically associated with water hyacinth in that system (Njiru *et al.*, 2004). Changes in prey preference could ultimately alter food web structure by decreasing populations of water hyacinth macroinvertebrates and increasing populations of former prey species.

In general, submerged macrophytes and roots from floating macrophytes provide shelter and cover for juvenile and small fishes that can enhance fish diversity (Johnson & Stein, 1979). In addition, an increase in epiphytic invertebrate abundance and diversity associated with water hyacinth may support a more diverse and larger fish community; however, this is not always the case. Water hyacinth mats can reduce natural predation and fisheries catchability, leading to increased abundance of certain species (Kateregga & Sterner, 2009); but mats can also exclude certain species from important breeding, nursery, and feeding grounds (Twongo & Howard, 1998).

Dissolved oxygen levels can reach dangerously low levels for fish when large water hyacinth mats prevent light infiltration or when a relatively large area of plants decompose at the

same time. Dissolved oxygen less than  $5 \text{ mg l}^{-1}$  are known to adversely affect function and survival of most fish, and less than  $2 \text{ mg l}^{-1}$  can lead to fish kills (Chapman, 1996). This is a major problem with some water hyacinth control techniques that leave plant material in the waterbody to decompose (Thayer & Ramey, 1986). Fish that are sensitive to changes in dissolved oxygen and plankton density may be less likely to persist in water-hyacinth-dominated systems; however, less-sensitive fish may be able to benefit from the provision of cover and an enhanced food supply by water hyacinth's complex root system. In a study on the effects of emergent and submerged vegetation on sunfish, fish abundance was directly related to dissolved oxygen concentrations within vegetated reservoir bays. Moreover, dissolved oxygen was inversely related to percent vegetation area cover, and dissolved oxygen levels were most sensitive to increasing vegetation cover at the vegetation-water edge and within dense vegetation; dissolved oxygen levels dropped below  $2 \text{ mg l}^{-1}$ , critically low for fish survival, in study bays when percent cover reached 50% (Miranda & Hodges, 2000). It is important to note that water hyacinth varies structurally and functionally from emergent and submerged vegetation because it is not anchored in the benthos. Therefore, one might expect the dissolved oxygen response to be different and therefore the effects on fish abundance and growth to differ as well.

Studies that have quantified the effects of water hyacinth on fish reported a range of results. Brendock *et al.*, (2003) found that fish diversity was higher at littoral sites with water hyacinth than without, although confidence in this result was dampened by variability associated with sampling techniques. On the St. Marks River in Florida, total fish abundance and biomass were similar within submerged vegetation in areas with and without a water hyacinth canopy, but species richness was significantly higher in areas with the water hyacinth canopy. Fish assemblages differed between sites with and without water hyacinth; notable differences

included the presence of two insectivorous fish species only found at sites with water hyacinth (Bartodziej & Leslie, 1998). After mechanical control of water hyacinth in a Mexican reservoir three common species (*Cyprinus carpio*, *Poecilia sphenops*, and *Heterandria jonesi*) disappeared. Mangas-Ramirez and Elias-Gutierrez (2004) suggested increases in nutrients as probable causes for the sudden fish population declines.

An important question to ask concerning the effects of water hyacinth on the fish community is, “How much water hyacinth is too much?” Several studies have shown a parabolic relationship between fish abundance and growth and emergent or submerged vegetation cover (Dribble *et al.*, 1996). This relationship is attributed to increased accessibility to prey, optimum protection from predators, and increased intra and inter-specific competition (Crowder *et al.*, 1982; Savino & Stein, 1982; Wiley *et al.*, 1984). Few studies have investigated the specific relationship between percent water hyacinth cover and the fish community. McVea and Boyd (1975) tested the effects of water hyacinth on fish productivity within 12 experimental ponds at Auburn University. By manipulating the percent cover of water hyacinth within each pond and stocking a fixed number of *Tilapia aurea*, they found that fish production was not affected by 5% water hyacinth cover, but 10 and 25% cover reduced production. In these cases, water hyacinth cover was indirectly affecting fish productivity via decreases in phytoplankton production with increased cover.

In summary, the response of the fish communities to water hyacinth is highly dependent on the pre-existing fish community, preferred and available fish habitat, food requirements and availability, physiochemical conditions and, likely although not proven, water hyacinth density

**Table 4: Results from studies that focused on the effects of water hyacinth (*Eichhornia crassipes*) or other macrophytes (Dribble *et al.*, 1996) on fish abundance, production, growth and community composition.**

<b>Author</b>	<b>Location</b>	<b>With water hyacinth</b>
Troutman <i>et al.</i> , (2007)	Atchafalaya River, Louisiana	Species composition different
Brendonck <i>et al.</i> , (2003)	Lake Chivero, Uganda	Fish diet increased in water hyacinth-associated insects
Bartodziej & Leslie, (1998)	St. Marks River, Florida	Different community composition; exclusive presence of 2 insectivore fish species
Mangas-Ramirez & Elias-Gutierrez, (2004)	Valsequillo Reservoir, Mexico	Loss of 3 common species after water hyacinth removal
Kateregga & Sterner, (2009)	Lake Victoria, Kenya, Tanzania, and Uganda	Decreased total fish catchability (2-45%)
Twongo & Howard, (1998)	Lake Victoria, Kenya, Tanzania, and Uganda	Blocked access to breeding, nursing, and feeding grounds for tilapia and young Nile perch  Increased abundance of <i>Haplochromines</i> and lungfish  Decreased abundance of tilapia
Dribble <i>et al.</i> , (1996)	Review paper	Intermediate vegetation cover yielded maximum fish growth and abundance
McVea and Boyd (1975)	Experimental ponds	< 10% water hyacinth cover had no effect on fish production  10-25% water hyacinth cover decreased fish production

(Table 4). The combination of these factors makes it very difficult to predict specific effects. However, given that dissolved oxygen concentrations decrease with increasing water hyacinth density, and given that macroinvertebrates and zooplankton are found at higher densities and in great diversity along the edges of water hyacinth mats, it is logical to suggest that fish could benefit from highly fragmented mats of water hyacinth. Such mats will have a higher edge-to-core ratio, providing some of the benefits of water hyacinth and minimizing the negative effects of dense non-fragmented mats.

### ***Waterbirds***

Despite the fact that waterbirds play an important role in aquatic food webs, research on water hyacinth effects on birds is sparse. Although little research has been conducted on the specific relationship between water hyacinth and birds (Haag *et al.*, 1987; Bartodziej & Weymouth, 1995), it is known that prey availability and habitat structure influence bird distributions (Murkin & Kadlec, 1986; Hoyer & Canfield, 1994; Bartodziej & Weymouth, 1995; Perry & Deller, 1996). Moreover, aquatic vegetation provides habitat structure, refuge from predators, and potential nursery habitat for aquatic invertebrates and fish that provide a prey base for many bird species (Haag *et al.*, 1987; Bartodziej & Weymouth, 1995; Svingen & Anderson, 1998; Brendonck *et al.*, 2003). Based on the assumptions stated above, we might expect higher bird density and diversity in freshwater systems invaded by water hyacinth that lack otherwise significant native vegetation. In systems with abundant native vegetation, the presence of water hyacinth may have little influence on the overall abundance of waterbirds, but could potentially shift bird community composition as a result of changes to habitat structure. Furthermore, there

is likely a density threshold at which waterbirds become negatively impacted by increasing water hyacinth. The threshold may be when dense mats physically prevent waterbird access to prey or if dissolved oxygen reductions cause negative effects on prey populations. Water hyacinth may become the dominant vegetative feature, outcompeting other vegetation types and resulting in a homogenous plant community that could restrict the diversity of the waterbird community.

According to an observational study conducted on St. Mark's River in Florida, birds that were seen feeding in water hyacinth mats more frequently found prey around the perimeter of the mats than within the core of the mats (Bartodziej & Weymouth, 1995). This is in agreement with studies that found higher densities of invertebrates within water hyacinth mats than other macrophyte stands or open water (Bailey & Litterick, 1993; Svingen & Anderson, 1998; Masifwa *et al.*, 2001a; Toft *et al.*, 2003) and greater abundance and diversity of macroinvertebrates along the plant-water interface (Masifwa *et al.*, 2001a). To date, there are no published studies that suggest water hyacinth mats affect the bird community or individual species; however, floating patches of water hyacinth appear to provide additional foraging habitat for large wading birds, such as the Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Tri-colored Heron (*Egretta tricolor*), and Great Blue Heron (*Ardea herodias*) (Villamagna, 2009).

### ***Control efforts***

Initial management of water hyacinth outside of its native range focused on eradication, but few success stories are known. Over time, management has shifted towards reducing plant density to levels that minimize economic and ecological impacts. Mechanical, chemical, and

biological control methods are commonly used to control water hyacinth, but no one method is suitable for all situations. Each method has advantages and disadvantages (Seagrave, 1988), and ultimately the choice of a control method should be based on site-specific conditions, including the size and spatial configuration of the area to be controlled (Thayer & Ramey, 1986), seasonal weather patterns, designated uses of the waterbody (Gibbons *et al.*, 1994), and budget constraints. Ultimately, the most sustainable solution for controlling water hyacinth outside of its native range would be broad-scale nutrient reduction plans (Musil & Breen, 1977); however, this would require extensive watershed-scale land-use changes and regulation that are inherently difficult, expensive, and politically complicated. In the sections to follow, we discuss the three dominant control methods, the ecological consequences of each, and provide several cases as examples.

### *Mechanical control*

Mechanical control options include harvesting plants and in-site cutting. There are several advantages and disadvantages to implementing a mechanical control strategy depending on the option chosen. In general, there are no water-use restrictions associated with mechanical control and it does not require much technical expertise. Mechanical control immediately opens physical space (habitat) for fish, boat traffic, fishing, and recreation. In-situ cutting, where plants are left to die and decompose in the water, can decrease dissolved oxygen and alter trophic structure as result of changes in nutrient and carbon balances (Scheffer *et al.*, 1993; Greenfield *et al.*, 2007). Moreover, low dissolved oxygen catalyzes the releases of phosphorous from the sediment and an increase in phosphorus often leads to a subsequent increase in water hyacinth or

algae blooms (Perna & Burrows, 2005; Bicudo *et al.*, 2007). While this is an obvious downfall of in-situ cutting, harvesting the plant can be costly and logistically difficult. Water hyacinth is comprised of approximately 90% water, making it very heavy to transport (Gopal, 1987). It also acts as a sink for heavy metals and other pollutants, therefore the issue of disposal and storage of decaying water hyacinth becomes an important health and ecological consideration once the plant is out of the water. Mechanical control may not be cost effective for extensive areas when large cutting or dredging equipment is required. Physical removal of water hyacinth may require establishment of an offsite disposal area, which can be more expensive than the removal process itself (Thayer & Ramey, 1986).

Following mechanical removal of water hyacinth from reservoirs in Brazil (within native range) and Mexico, water transparency and dissolved oxygen decreased, while pH, total phosphorus, phytoplankton, and cyanobacteria biomass (*i.e. Mycrocystis spp.*) increased (Mangas-Ramirez & Elias-Gutierrez, 2004; Bicudo *et al.*, 2007). The Brazilian reservoir shifted to a persistent state dominated by cyanobacteria (Bicudo *et al.*, 2007). Decreases in dissolved oxygen concentrations were linked to mass decomposition of phytoplankton and cyanobacteria following blooms. In contrast, mechanical harvesting of water hyacinth from an Australian lagoon resulted in a sudden increase in dissolved oxygen (Perna & Burrows, 2005), which was possibly due to higher water flow rates in the lagoons than in the reservoirs.

### *Chemical Control*

Chemical control plans have been introduced in several locations worldwide; Glyphosate (Roundup), Diquat, and 2, 4-D amine are common herbicides used on water hyacinth (Seagrave,

1988; Gutierrez *et al.*, 1994; Lugo *et al.*, 1998). Chemical control plans are considered less labor intensive and less expensive than mechanical control, especially at large scales (Gutierrez-Lopez 1993). Although chemical control plans can cover large areas in short time periods, herbicides can become expensive if management requires repeated applications. The cost of the chemical plan will depend heavily on the equipment used to administer the herbicide (e.g. backpack sprayer, helicopter, or airboat). Spraying large areas within a short time span can cause dangerous deoxygenation of water (Lugo *et al.*, 1998). Herbicides are less selective than mechanical or manual approaches and can kill non-target algae and macrophytes (Seagrave, 1988), resulting in far reaching ecological impacts (Richards *et al.*, 1985; Arora & Mehra, 2003; Rocha-Ramirez *et al.*, 2007). The herbicide should be sprayed directly onto the leaves of water hyacinth to avoid killing algae in the water column (Seagrave, 1988).

Following mechanical control and the application of diquat and 2, 4-D amine to a Mexican reservoir, algae, pH, and dissolved oxygen increased (Lugo *et al.*, 1998). Olaleye (2002) reported similar results from laboratory experiments. A chemical control programme in a Nigerian creek produced a significant increase in fish abundance 14 days after treatment (Olaleye, 1993). The increase was assumed to be a result of the removal of plant barriers to fish movement. However, not all fish species experienced a significant population increase following treatment, suggesting other factors driving fish distribution.

A final consideration with the implementation of a chemical control plan is the water use restrictions that may be required by law following herbicide spraying. The implementation of a chemical control plan can have significant socio-economic impacts if beneficial or designated uses of the waterbody are affected.

## *Biological control*

Biological control is an attractive alternative to mechanical and chemical control programmes because it avoids the introduction of toxic chemicals, it is not labor or equipment intensive, and it has the potential to be self-sustaining if the introduced biological agent can reproduce successfully in the new environment without causing further ecological effects (Seagrave, 1988). Much of the cost of biological control programmes is on the front end, mainly related to research and development. Biological controls are often viewed as a long-term, sustainable solution to water hyacinth control. Host specificity is critical to any successful biological control programme. Ideally, the introduced agent will have a narrow range of requirements to keep the effects focused on the target plant but broad enough to maintain a viable population when the host plant is in low densities. Common biological control options for water hyacinth include various insect species and introduced plant pathogens (Coetzee *et al.*, 2007). *Neochetina eichhorniae* and *N. bruchi* are two commonly used weevil species from the plant's native range (Sosa *et al.*, 2007). To date, fish are not known to control water hyacinth (Seagrave, 1988). Biological control is commonly preceded by mechanical removal or chemical treatment in order to quickly reduce the population, making initial conditions suitable for effective biological control (Adekoya *et al.*, 1993). In cases where *Neochetina spp.* is introduced, population control of water hyacinth is not realized for many years. In tropical systems, biological control is thought to take 3-5 years to become effective (Harley, 1990); in Lake Victoria it took four years for introduced *Neochetina* to significantly decrease water hyacinth cover (Wilson *et al.*, 2007). Thus far, weevil-based control has been less effective in colder temperatures (Hill & Olckers, 2001; Coetzee *et al.*, 2007); therefore its use has been limited to tropical and sub-tropical regions.

In general, water quality impacts of biological control methods appear quite similar to other removal techniques. *Neochetina* weevils reduce water hyacinth buoyancy, causing plants to sink to the bottom and decompose (Wilson *et al.*, 2007). While this process may not drastically affect water quality in deep areas or where large mats of water hyacinth do not sink at once, shallow areas are more vulnerable to the negative effects associated with the decomposition of plants. One of the advantages of a biological control programme is the potential for it to become a self-sustaining aspect of ecosystem function. However, it is still a non-native component introduced to the ecosystem, and it has the potential to affect other aspects of the ecosystem (Simberloff & Stiling, 1996).

### **Socio-economic effects of water hyacinth**

There is a dichotomy of socio-economic impacts associated with invasive species. There are the benefits and costs that result from the presence of water hyacinth, and there are the benefits and costs of preventing, managing, or eradicating the species, including the ecological impacts of those actions.

From a socio-economic perspective, water hyacinth invasion into freshwater systems presents a problem for many human uses. The most direct impacts are to boating access, navigability, and recreation; and to pipe systems for agriculture, industry, and municipal water supply. Access to fishing grounds and fish catchability are also affected (Kateregga & Sterner, 2009). Furthermore, evapotranspiration from water hyacinth can exceed open-water evaporation rates by a factor of ten in some areas (Gopal, 1987). This can be a serious concern in water-limited areas and small waterbodies. Water hyacinth can greatly affect a fishery if it induces

changes in fish community composition, or if catchability of harvested species is changed. In Lake Victoria, fish catch rates decreased because water hyacinth mats blocked access to fishing grounds, delayed access to markets, and increased fishing costs (effort and materials) (Kateregga & Sterner, 2009). Mats also blocked breeding, nursery, and feeding grounds for economically important species, such as tilapia and Nile perch in Lake Victoria (Twongo & Howard, 1998). It is interesting to note that decreased catchability of certain overfished species can lead to increased fishery stocks (Kateregga & Sterner, 2009) that in the long-run could benefit a fishery and human society.

The socio-economic impacts of water hyacinth will also vary in relation to the uses of the waterbody. An infestation will likely have a greater socio-economic impact when the waterbody supports several human uses. For a system that is primarily used as a water source, impacts could be measured in terms of changes to water quality. While it is inherently difficult to assign a value to the loss of water quality, a surrogate estimate can be used. In this example, any change in the cost of water treatment could be considered a substitute economic value. This technique is referred to as the replacement cost method (Holl & Howarth, 2000). In addition to beneficial economic uses, there are also the impacts on wildlife and ecosystem services; such impacts are not usually reflected in our traditional economic market system. A non-market approach, such as contingent valuation, can be used to account for these impacts (Holl & Howarth, 2000). Contingent valuation is a relatively time-consuming option, and therefore it is likely under-used in attempts to quantify the costs and benefits of invasive species. It is also important to recognize that biological impacts and socio-economic impacts may not be immediately realized. Instead damages may increase over time or as a result of synergistic biological or economic interactions (Parker *et al.*, 1999). For example, reduced dissolved

oxygen may occur as a result of dense water hyacinth mats, but it is the risk of fish kills that would likely draw socio-economic attention. Accounting for all of the impacts is inherently challenging; however, in a world where the invasive species are rapidly increasing, we should begin to prioritize management efforts.

The economic cost of controlling water hyacinth infestations is a function of the rate of removal, cost of labor, cost of equipment, and the frequency of treatment. Each of these factors will vary based on the extent of the infestation and the type of control used. Since some methods have more immediate effects on the water hyacinth population, the planned rate of removal should incorporate any time lags that may exist between treatment and effect. This complicates what appears to be a simple analysis because the rate of removal may change over time; for example, biological control requires time to build a large enough population of the biological agent to have significant effects on the water hyacinth population (Center, 1994; Center *et al.*, 1999). In terms of invasive plant management, perhaps the most important factor to consider is time of regrowth. Many management decisions are made based on ‘least-cost control’ without consideration for the temporal duration of control efforts. This is most important in systems where permanent eradication is not a feasible option. Mechanical shredding of water hyacinth is cheaper than harvesting (Greenfield *et al.*, 2006), but there are significant consequences of allowing the plant to die and decompose within the system. Although mechanical control may initially be less expensive than an herbicide treatment, over time the chemical control may cost less due to the slower regrowth time associated with the herbicide treatments. However, in countries like the US, recent permitting and monitoring requirements associated with a chemical control programme may significantly increase the overall cost of implementation (Greenfield *et al.*, 2007).

## **Discussion**

Our review of the water hyacinth literature from the past 30 years makes it clear that there is little consistency among field studies and experiments that focus on the effects of water hyacinth. One of the most common differences among studies was the time frame during which impacts were analyzed. Some studies focused efforts on comparing sites with and without water hyacinth, while others examined the effects of water hyacinth removal. There are very few studies that report pre-invasion ecological condition. The overall inconsistency in the nature of these studies makes it extremely difficult to make broad, sweeping conclusions.

There remain several unknowns with regards to water hyacinth invasions. Perhaps the most obvious information gap exists with respect to the effects of water hyacinth density on ecosystems. Water hyacinth density or percent cover was rarely reported in the papers reviewed, with the exception of an experimental-pond study (McVea & Boyd, 1975). Without such information it is difficult for a manager to establish management goals for the control of water hyacinth. It is also difficult to know when, in terms of density or percent cover, water hyacinth control is a necessity in order to prevent ecological or socio-economic damage. Moreover, this information could help managers increase lake productivity by harnessing the positive impacts of water hyacinth (e.g. habitat structure, refuge area, and nutrient reductions). We also lack a strong understanding of the effects of water hyacinth and many other invasive aquatic plants on the waterbirds. Birds comprise the highest trophic level in many systems, and thereby can reflect the condition of the ecosystem as a whole. The density threshold at which water hyacinth starts to impact ecosystems, society, and local economies are also not known. Understanding these thresholds will help management establish goals for population control that can maximize the social benefits while minimizing the costs of the invasive species.

From these gaps we suggest the development of ecosystem-level research programmes that simultaneously monitor the effects of water hyacinth on multiple trophic-levels, especially waterbirds (i.e. from water quality impacts up to waterbird impacts); these programmes will help us understand the direct and indirect impacts that water hyacinth may have on ecosystems. We also suggest the development of experimental studies that will mimic different invasion patterns and management scenarios (e.g. determining the ecological threshold at which water hyacinth density or percent cover begins to change ecological function or food web structure). Similarly, it would be helpful to test different water hyacinth control plans to identify those that produce the most desired outcomes. For this we suggest varying overall reductions (percent cover or density), spatial dimensions of removal (e.g. removing strips or channels in water hyacinth mats to increase edge), and timing of control efforts; temporal variation in control efforts could greatly affect the response of water hyacinth and the ecosystem as a whole, and this should be incorporated in management-oriented research.

At a broader scale, we suggest research that focuses on the potential spread of water hyacinth into northern latitudes as a response to global climate change (Hellmann *et al.*, 2008; Rahel & Olden, 2008). Finally, more research is needed on alternatives for the sustainable management of this worldwide invader; this includes economic incentives for private removal, spread prevention, or utilization projects that create goods from water hyacinth. In conclusion, our understanding of water hyacinth is still relatively weak, and hinders our ability to manage systems appropriately where this invader occurs. With the likely spread of aquatic invaders due to climate change, it is imperative that we continue and refine our water hyacinth research efforts to reflect better the needs of managers.

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## Chapter 2

### Effects of water hyacinth cover on the waterbird community of Lake Chapala, Mexico

**Keywords** Water hyacinth, *Eichhornia crassipes*, Waterbirds, Community composition, Species Diversity, Habitat use

#### INTRODUCTION

Invasive species are considered to be a leading threat to global aquatic biodiversity (Mack et al. 2000). While these species can cause economic and ecological damage, non-native species can also stimulate ecological and economic ‘benefits’ in some circumstances (Twongo and Howard 1998, Kateregga and Sterner 2009). While the costs and benefits of invasive species may be situation-specific (Lockwood and Latchininsky 2008), the introduction of non-native species will continue to accelerate with increasing interaction among water bodies worldwide (Millenium Ecosystem Assessment 2005), thus making invasive species management more challenging and prioritization more important.

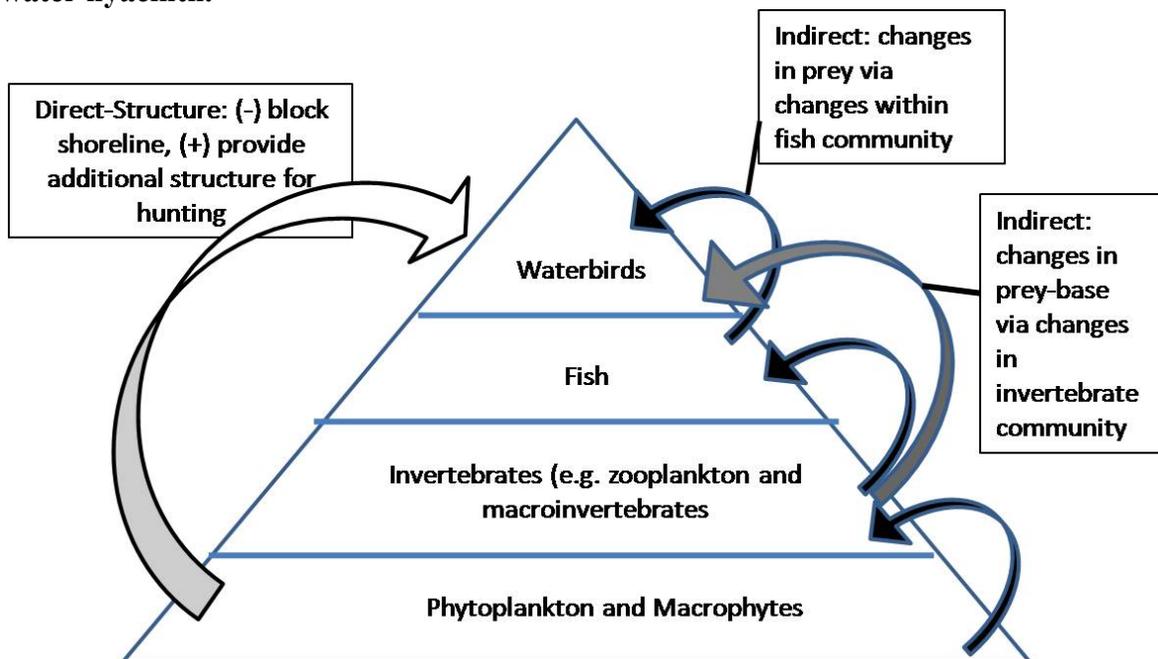
Water hyacinth (*Eichhornia crassipes*) is an invasive aquatic plant associated with a variety of ecological and economic effects on freshwater ecosystems (Center 1994). Water hyacinth is considered to be one of the most invasive aquatic species in the world. Originally from South America, it is currently found on five continents within tropical and subtropical freshwater regions (Bartodziej and Weymouth 1995, Brendonck et al. 2003, Lu et al. 2007, Martinez Jimenez and Gomez Balandra 2007). It is a free-floating aquatic macrophyte that clusters in large mats that block shorelines and congest coves (Mitchell 1985). Water hyacinth is known to decrease phytoplankton productivity leading to decreases in dissolved oxygen; low

dissolved oxygen can have negative consequences for fish and other waterbird prey under these mats (Meerhoff et al. 2003, Toft et al. 2003). Another lesser known effect of water hyacinth include its ability to remove nutrients and contaminants from the water (Aoi and Hayashi 1996, Tiwari et al. 2007, Zimmels et al. 2007). It is known to increase invertebrate abundance and diversity by providing habitat within its complex root system (Brendonck et al. 2003, Toft et al. 2003). The dense and intricately connected root system also provides refuge and nursery habitat for small and juvenile fish as well as zooplankton (Brendonck et al. 2003).

Much of the research to date has focused on the effects of water hyacinth on lower trophic communities (e.g. invertebrates and fish) but little attention has been specifically paid to the effects on waterbirds (Gibbons et al. 1994). The lack of information pertaining to waterbirds prevents full understanding of the effects of water hyacinth, making it difficult to choose appropriate management action and to assess success. There are several ways that water hyacinth could directly and indirectly affect waterbird communities (Figure 1). Despite the apparent knowledge gap with respect to invasive aquatic plants and waterbirds, we know that waterbird distribution is highly dependent on habitat structure, prey availability, and the presence of conspecific species (Bartodziej and Weymouth 1995, Martinez 2004). Therefore, if a non-native plant provided habitat that was unsuitable for a particular bird species or the community as a whole we might expect an inverse relationship between water hyacinth cover and waterbird abundance or diversity (Figure 2a). However, prior studies suggest that aquatic vegetation in general and water hyacinth specifically provide habitat for invertebrate and fish production (Haag et al. 1987, Bartodziej and Weymouth 1995, Svingen and Anderson 1998, Brendonck et al. 2003), which suggests a potential positive relationship between water hyacinth cover and waterbirds abundance or diversity (Figure 2b). Yet, based on the effects of water hyacinth on

dissolved oxygen, it seems likely that this positive relationship might deteriorate when water hyacinth is very abundant, suggesting a parabolic relationship (Figure 2c). This parabolic relationship was suggested for breeding waterfowl in prairie marshes by Weller and Spatcher (1965). The hemi-marsh concept suggests that waterfowl and invertebrate use of marsh areas was highest when open water and emergent vegetation were roughly equal in area. A similar relationship is suggested between fish and macrophytes, where fish abundance is maximized at intermediate levels of plant cover (Miranda and Hodges 2000). At first, fish abundance increases as vegetation increases prey abundance and provides refuge from predators; then increased intra- and interspecific competition and decreased dissolved oxygen concentrations limit or decrease fish abundance. Barring other contributing factors, we might expect overall waterbird abundance

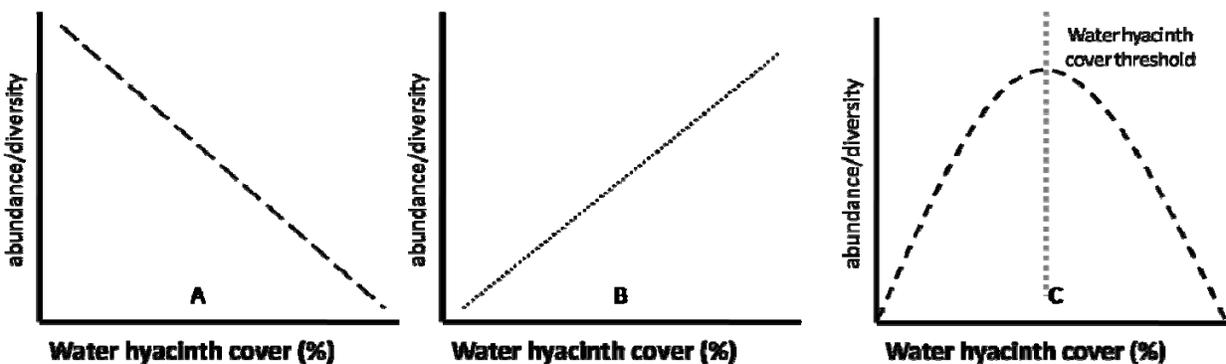
**Figure 1: A suite of direct and indirect ecological effects associated with the establishment of water hyacinth.**



and diversity in Lake Chapala to follow suit. The threshold at which water hyacinth cover and waterbird abundance become inversely related may vary among species based on the species'

habitat requirements and feeding strategy (Esler 1992, Whitt et al. 1999, Maddox and Wiedenmann 2005). For example, Pied-billed Grebes (*Podilymbus podiceps*) were found in higher densities within Hydrilla (*Hydrilla verticillata*), another common aquatic invasive plant, than open water, but a significant difference was not detected for other piscivores like the Cormorant (*Phalacrocorax spp.*) and American Pelican (*Pelecanus erythrorhynchos*; Esler, 1992). Whitt *et al.* (1999) found ten species of native birds breeding in marsh areas dominated by purple loosestrife (*Lythrum salicaria*), an understudied invasive plant in Eurasia. Swamp Sparrows (*Melospiza Georgiana*), Blue-winged-Teals (*Anas discors*), Mallards (*Anas platyrhynchos*), and Red-winged Blackbirds (*Agelaius phoeniceus*) were found nesting in purple loosestrife. Prior to this study, many assumed that this invasive plant was of little value to breeding birds. Moreover, Wicker and Endres (1995) found that Eurasian watermillfoil (*Myriophyllum spicatum*), an invasive submerged macrophyte, supported high densities of dabbling ducks and American Coots in the Currituck Sound, North Carolina (USA).

**Figure 2: Potential waterbird responses to water hyacinth cover.**



In this study, I investigated potential relationships between water hyacinth cover and the waterbird community of Lake Chapala. Specifically, I test for relationships between water hyacinth cover and 1) site-level waterbird abundance, 2) site-level abundance of the four most

common species, 3) species diversity, 4) waterbird community composition, and 5) use of water hyacinth habitat by all species identified at Lake Chapala during this study. I calculated diversity using Simpson's index that calculates a value for diversity (between 0 and 1) based on the number of species present and the abundance of each species (evenness). Community composition refers to the identity of species and abundance of each species. Community composition may differ between sites while the diversity index remains the same because the former takes into account which species are occurring. The objectives of this study were to determine whether water hyacinth affected 1) abundance, 2) species diversity, 3) community composition, and 4) proportional water hyacinth use of waterbirds at the site level.

## **METHODS**

### **Study site**

Lake Chapala is the largest freshwater lake in Mexico, covering approximately 112,000 ha (CEA-Jalisco 2008). The Lerma River is the main inflow for Lake Chapala and the main channel for the Lerma-Chapala watershed that crosses through five states. The lake itself is bordered by the states of Jalisco and Michoacán. Lake Chapala is a shallow tropical lake that is considered eutrophic in terms of nutrient enrichment, yet has low primary productivity due to high turbidity (Davalos-Lind and Lind 2001, Lind and Davalos-Lind 2001). Water hyacinth is found along shorelines and as floating mats surrounded by open water (patch water hyacinth). Its mobility causes its distribution throughout the lake to change daily in response to wind and water currents. Water hyacinth has been present in the system for about 100 years during which time

several management approaches have been taken. This study took place during a time of major change at Lake Chapala with respect to the water hyacinth population. Organized chemical control efforts began about mid-way through the study, first observed in winter 2007. Water hyacinth was most abundant in winter 2007 and decreased throughout the remainder of the study. During winter and summer 2008 there was on average less than 3% water hyacinth cover at all study sites. The lake also experienced a severe drought in summer 2007 that increased open shoreline habitat area.

#### Abundance and species diversity

I examined the relationship between water hyacinth cover and the waterbird community on Lake Chapala, Mexico by comparing waterbird assemblages in areas with and without water hyacinth. I monitored waterbird habitat use and estimated daily water hyacinth cover at 22 sites during 7 consecutive sampling seasons between May 2006 and June 2008 (Table 1). Sites were randomly selected from the lake using a grid overlay and random number table; however, site access limited the final site selection (Figure 3). The size and shape of sites varied slightly due to different landscape features, but the distance from shore was standardized (100 m from shore). Sites were visited 4-8 times each season. Water hyacinth cover was estimated for each site visit using aerial photos and ground surveys. Aerial photos provided the initial layout of a site and basis for calculating lake surface cover by water hyacinth. I calculated a percent of site cover because the absolute site area changed within a season and drastically throughout the study due to changing lake water levels. I calculated site water hyacinth cover from the ground using

**Table 1: Waterbird study seasons at Lake Chapala, Mexico.**

Season	Dates
Summer 2006	June 6-20, 2006
Fall 2006	September 28-October 9, 2006
Winter 2007	February 2-23, 2007
Summer 2007	May 24-June 29, 2007
Fall 2007	September 26-October 14, 2007
Winter 2008	January 29-February 22, 2008
Summer 2008	May 28-June 23, 2008

landscape references provided by the aerial photos. I used a spotting scope (15-60 x) and binoculars (8 x 48 mm) to identify and count waterbirds at each site. I identified birds by species and recorded the habitat in which they were found (Table 2). Surveys lasted up to 20 minutes at each site depending on water hyacinth cover and weather. I started identifying birds at one end of the site and continued in the opposite direction (scan sampling) to avoid double counting (Hepworth and Hamilton 2001).

**Figure 3: Twenty-two randomly selected study sites around Lake Chapala, Mexico.**



**Table 2: Description of waterbird habitat types classified around Lake Chapala, Mexico.**

Habitat Type	Description
Open water	Water without vegetation
Patch water hyacinth	Water hyacinth mats surrounded by water on all sides
Emergent vegetation	Rooted vegetation including cattail and bulrush
Shoreline water hyacinth	Water hyacinth mats clustered along shoreline
Open shoreline	Shoreline without water hyacinth, mainly mud, cobble, and grass
Shallow water	Water less than 0.5 m deep
Rocks	Rocks above the surface of the water
Submerged trees	Stumps and trees surrounded by water; sometimes with foliage.

I tested the relationship between waterbird abundance and water hyacinth cover using Kendall's Tau Correspondence Test ( $\alpha=0.05$ ). This is a non-parametric statistical test that measures the correspondence between rankings and does not assume any prior distribution. I chose this non-parametric test because the data were non-normally distributed and could not be linearly transformed for all study seasons. I determined the four most abundant species at Lake Chapala during this study, calculated mean seasonal abundance, and tested for a relationship between individual species abundance and percent water hyacinth cover. Using the same statistical approach, I tested for a relationship between species diversity (Simpson's index of diversity: Krebs, 1999) and percent water hyacinth cover during each site-visit. I calculated Simpson's index of diversity for winter 2007 and 2008 with and without migratory birds included to avoid potential bias caused by the influx on non-resident birds. For all analyses described, I tested for these relationships separately for each season to account for seasonal differences in temperature, precipitation, and other underlying conditions that were not explicitly included in the model. The correspondence coefficient (Tau) and the P-value for each season are reported.

### Community composition

I used Canonical Correspondence Analysis (CCA) to test the relationship between water hyacinth cover and waterbird community composition. CCA tests whether community composition is more strongly influenced by water hyacinth cover than by chance. This analysis requires species data and environmental data for each site. It plots species composition and water hyacinth cover in a three-dimensional space and searches for patterns in community

structure explained by water hyacinth cover (Ter Braak and Prentice 1988). I aggregated the data (seasonal-site averages for individual species abundance and water hyacinth cover) to reduce the number of zeros in the data set, thereby increasing the effectiveness of the CCA (Lira-Noriega et al. 2007). I ran a Monte Carlo simulation ( $n = 998$ ) using eigenvalues of the axes to test the null hypothesis that there is no relationship between water hyacinth cover and waterbird community structure. Community composition analyses were conducted for each season separately using PC-Ord statistical software (McCune 2002)

#### Proportional water hyacinth use

I studied habitat use by waterbirds on Lake Chapala to better understand the habitat-level effects of water hyacinth. In this study, I define ‘use’ as a bird being present on or within a given habitat type. Specifically, the objective was to determine if waterbirds use water hyacinth as much as expected (i.e. null hypothesis), select for it, or select against it (avoidance). The species-level response is important to consider if there are species of particular management concern. During each of the site surveys I recorded the abundance of various waterbird species present within water hyacinth and present within the entire site. I used daily percent cover of water hyacinth to calculate the habitat selection ratio (Equation 1),

$$R_{ijk} = \frac{(C_{ijk} / C_{i.k})}{P_{jk}}$$

(Equation 1)

where  $C_{ijk}$  is the total number of species  $i$  observed in habitat  $j$  (water hyacinth) at site  $k$ ,  $C_{i,k}$  is the total number of species  $i$  observed at site  $k$ , and  $P_{jk}$  is the percent water hyacinth cover observed at site  $k$  during that visit (Manly et al. 1993). I then calculated the overall resource selection ratio  $R_{ij}$  by averaging  $R_{ijk}$  over all site visits within a given season, where  $n$  is the number of observations made for that species during that season (Equation 2). I removed records where no individuals of a given species were observed during a particular site visit.

$$R_{ij} = \frac{\sum_{i=1}^n R_{ijk}}{n}$$

(Equation 2)

I calculated 95% confidence intervals around the overall habitat selection ratio (Equation 3) to determine if a given species significantly selected for or against water hyacinth. If the lower confidence limit was  $> 1$ , then that species significantly ( $p < 0.025$ ) selected for water hyacinth; if the upper confidence limit was  $< 1$ , then the species significantly ( $p < 0.025$ ) selected against or avoided water hyacinth.

$$se(R_{ij}) = \sqrt{\frac{\sum_{i=1}^n (R_{ijk} - R_{ij})^2}{n-1}}$$

(Equation 3)

## RESULTS

### Abundance

The waterbird community of Lake Chapala was comprised of 23 species during this study, nine of which were winter migrants (Table 3). I found that waterbird abundance corresponded positively with water hyacinth cover during fall 2006 and 2007 (Table 4) but not during any other season. Fall 2006 and 2007 were seasons of moderate to high water hyacinth cover (Figure 4) with a seasonal site average of 14.7% water hyacinth during fall 2006 and 10.4% in fall 2007. The four most abundant species I observed in this study include the Great Egret (*Ardea alba*), the Snowy Egret (*Egretta thula*), the Great Blue Heron (*Ardea herodias*), and the American Coot (*Fulica americana*) (Figure 5). I found significant positive correspondence between abundance and water hyacinth cover for all four species during at least one study season. I only found a significant inverse relationship between water hyacinth and individual species abundance for the American Coot in fall 2007 (Table 5).

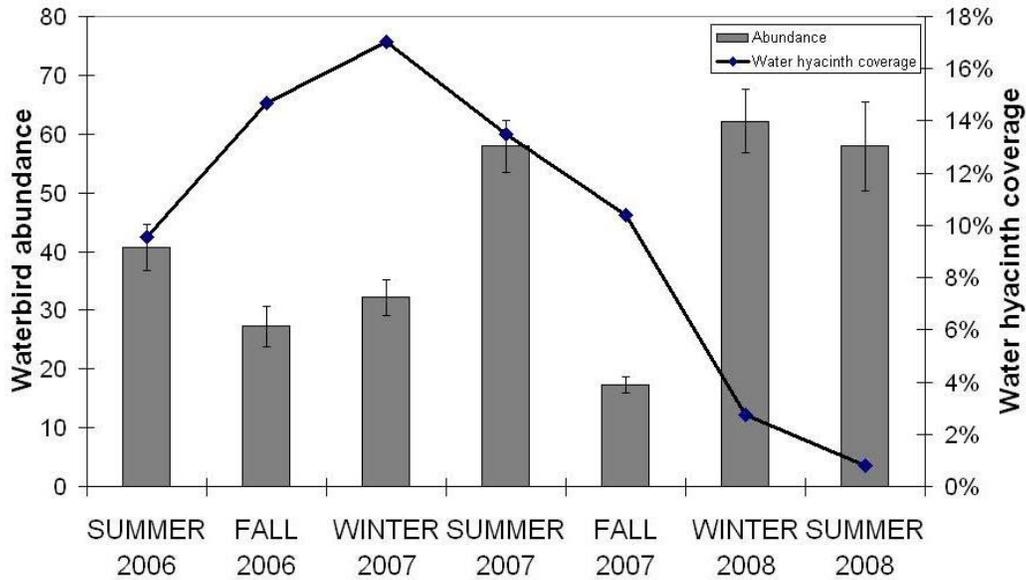
### Species diversity

Mean species diversity varied significantly by season ( $p < 0.0001$ ; figure 5) but there was little intra-season variability (diversity index standard error = 0.02). Highest diversity was observed during summer 2006 and winter 2008 when migratory birds were excluded from the calculation (Figure 6). The diversity index was lowest for all seasons in winter 2008 when migratory birds were included (Simpson's index of diversity = 0.51; Figure 6). I found a

**Table 3: Latin and common name for birds observed at Lake Chapala, Mexico between May 2006 and June 2008. (\*) denotes wintering species.**

<b>Species</b>	<b>Common Name</b>
<i>Fulica americana</i>	American Coot
<i>Gallinula chloropus</i>	Common Moorhen
<i>Jacana spinosa</i>	Northern Jacana
<i>Ardea alba</i>	Great Egret
<i>Ardea herodias</i>	Great Blue Heron
<i>Egretta thula</i>	Snowy Egret
<i>Nycticorax nycticorax</i>	Black-crowned Night Heron
<i>Egretta caerulea</i>	Little Blue Heron
<i>Egretta tricolor</i>	Tricolor Heron
<i>Butorides virescens</i>	Green Heron
<i>Bubulcus ibis</i>	Cattle Egret
<i>Phalacrocorax spp.</i>	Cormorant
<i>Charadrius vociferus</i>	Killdeer
<i>Platalea ajaja</i>	Roseate Spoonbill
<i>Himantopus mexicanus</i>	Black-necked Stilt
<i>Anas diazi</i>	Mexican Duck
<i>Calidris spp.</i>	Sandpiper*
<i>Gallinago gallinago</i>	Common Snipe*
<i>Anas discors</i>	Blue-winged Teal*
<i>Anas cyanoptera</i>	Cinnamon Teal*
<i>Anas clypeata</i>	Northern Shoveler*
<i>Anas strepera</i>	Gadwall*
<i>Anas acuta</i>	Northern Pintail*
<i>Pelecanus erythrorhynchos</i>	American Pelican*

**Figure 4: Mean seasonal waterbird abundance at the site-level compared to mean seasonal water hyacinth cover at the site-level for Lake Chapala, Mexico. Bars represent mean seasonal waterbird abundance, error bars illustrate standard error, and the line illustrates mean seasonal water hyacinth cover.**



**Table 4: The correspondence between daily water hyacinth cover and site-level waterbird abundance at Lake Chapala, Mexico.**

Season	Kendall Correspondence Coefficient	P-value
Summer 2006	0.165	0.08
Fall 2006	0.399	< 0.0001*
Winter 2007	0.036	0.62
Summer 2007	0.017	0.75

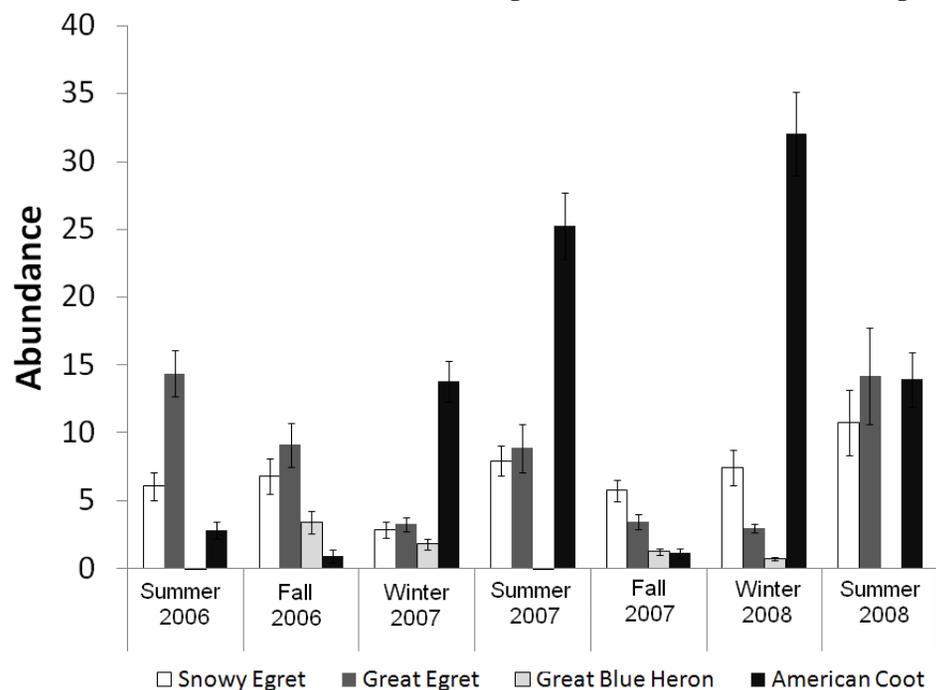
significant positive correspondence between water hyacinth cover and waterbird species diversity during the 2008 winter season (with and without wintering birds) and an inverse correspondence during summer 2006 (Table 6 & Figure 6); however, only 12 sites were

surveyed during summer 2006 before 10 additional sites were added to strengthen statistical power. The positive correspondence within winter 2008 and the low seasonal water hyacinth cover (2.75%; Figure 4) may suggest a low threshold at which species diversity was affected by water hyacinth cover. In other words, certain species may have been precluded from sites with low water hyacinth cover. The relationship may be much weaker beyond this threshold, explaining the lack of a positive correspondence in winter 2007 and other seasons with relatively abundant water hyacinth cover. I tested the correspondence relationship at different cover increments during winter 2007, when mean water hyacinth cover was greatest (17.5%), to determine if a threshold existed for species diversity. I focused on winter 2007 to maximize comparability with winter 2008 by minimizing potential variability associated seasons not accounted for in this study. I tested for a relationship when water hyacinth cover was less than 5%, 10%, and 25%. None were statistically significant (Table 7), suggesting that there was no detectable diversity threshold associated with water hyacinth cover in winter 2007.

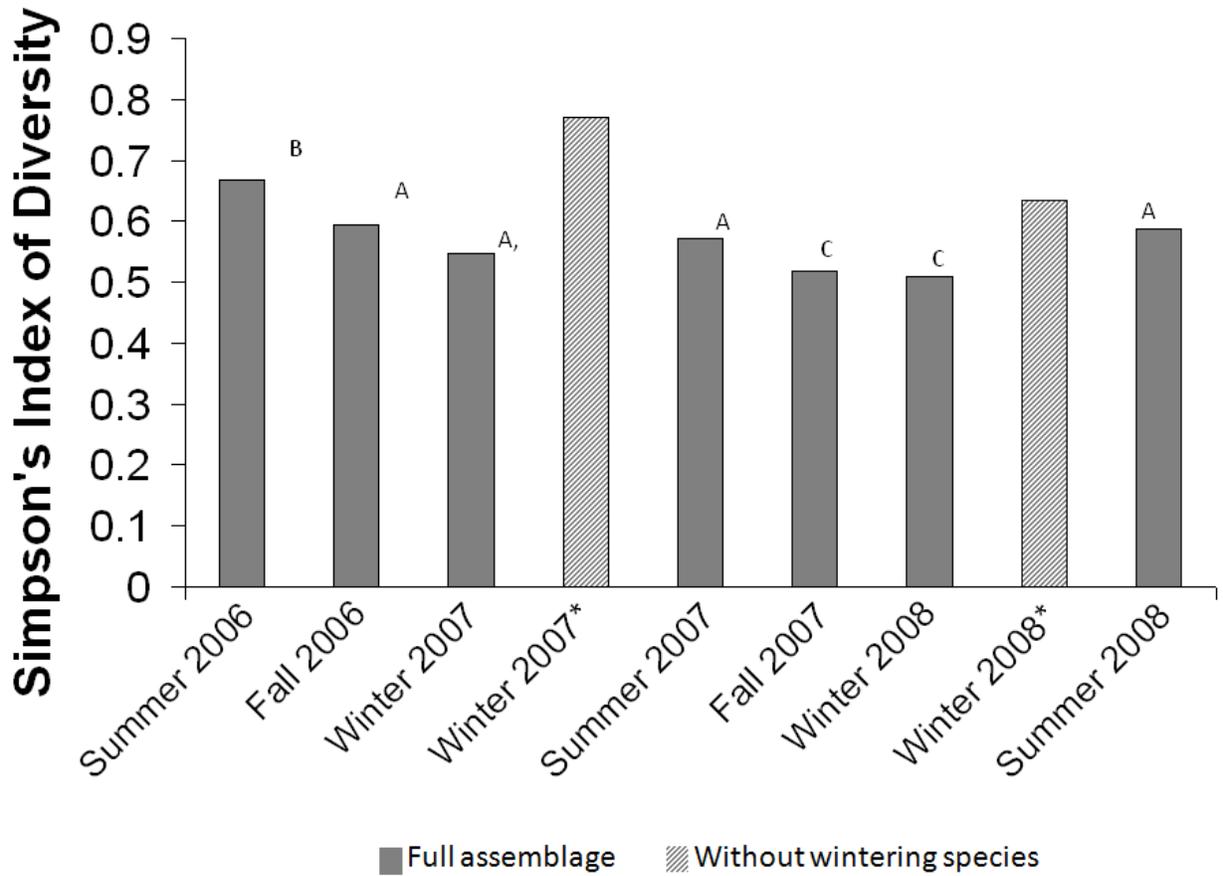
**Table 5: The correspondence between daily water hyacinth cover and site-level species abundance for the four most abundant species at Lake Chapala, Mexico.**

	Summer 2006		Fall 2006		Winter 2007		Summer 2007		Fall 2007		Winter 2008		Summer 2008	
	tau	P	tau	P	tau	P	tau	P	tau	P	tau	P	tau	P
Snowy Egret	0.02	NS	0.19	0.03	-0.08	NS	-0.03	NS	0.17	0.005	0.14	0.05	0.03	NS
Great Egret	0.16	NS	0.47	<.0001	0.12	NS	-0.02	NS	0.24	0.0001	0.13	NS	0.03	NS
Great Blue Heron	0.01	NS	0.36	<.0001	0.11	NS	-0.03	NS	-0.02	NS	0.03	NS	NA	NA
American Coot	-0.25	0.01	0.13	NS	-0.04	NS	-0.02	NS	-0.18	0.01	-0.08	NS	-0.12	NS

**Figure 5: Mean site-level abundance for the four most abundant species observed at Lake Chapala during this study.**



**Figure 6: Mean waterbird diversity for all site visits by season at Lake Chapala, Mexico. Seasons with different letters differ significantly in Simpson's diversity index. Winter diversity was calculated with and without migratory wintering species.**



**Table 6: The correspondence between daily water hyacinth cover and site-level species diversity at Lake Chapala for all study seasons.**

Season	Kendall Correspondence Coefficient	P-value
Summer 2006	-0.299	0.003*
Fall 2006	-0.096	0.25
Winter 2007	-0.033	0.65
Winter 2007 (no migrants)	0.012	0.86
Summer 2007	0.043	0.43
Fall 2007	0.032	0.59
Winter 2008	0.170	0.01*
Winter 2008 (no migrants)	0.142	0.03*
Summer 2008	0.020	0.78

**Table 7: Threshold tests for correspondence between daily water hyacinth cover and site-level species diversity at Lake Chapala, Mexico for all study seasons**

Water hyacinth cover	Sample size	Kendall' Correspondence Coefficient	P-value
< 5%	26	-0.013	0.93
< 10%	36	-0.02	0.87
< 15%	52	0.007	0.94
< 25%	74	-0.049	0.54

#### Community composition

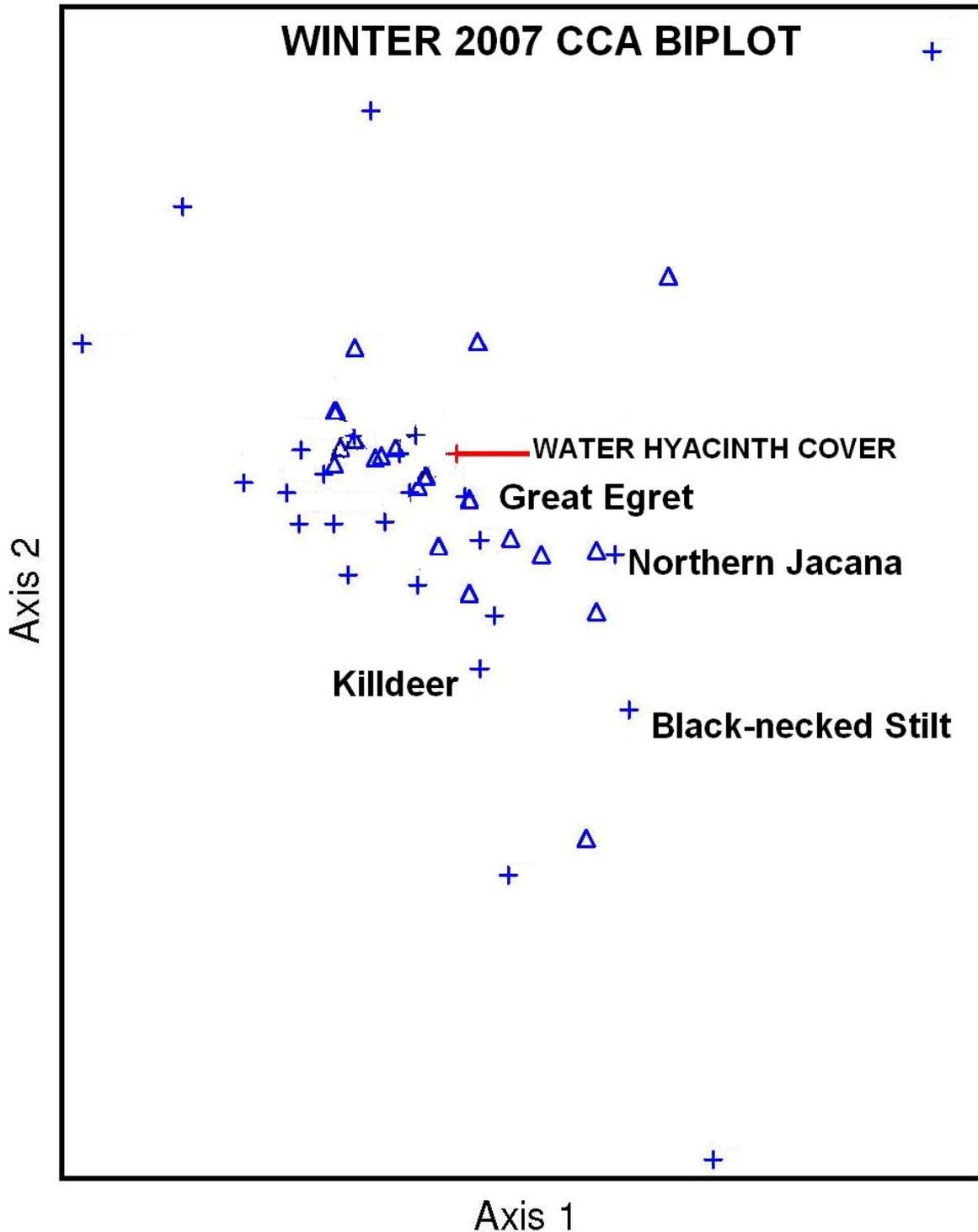
Waterbird community composition corresponded significantly with water hyacinth cover during winter 2007. Winter 2007 had the highest seasonal water hyacinth cover (17.5%) but only moderate mean waterbird species diversity (Figure 5). The Canonical Correspondence

Coefficient of axis 1 in this analysis was notably greater, suggesting a stronger relationship between water hyacinth cover and waterbird community composition than observed in other seasons. The Monte Carlo simulation validated the significance of the correspondence ( $P = 0.007$ ). Notable trends from the winter 2007 CCA biplot (Figure 7) include a positive relationship between water hyacinth and Great Egret, Northern Jacana, Killdeer, and Black-necked Stilt abundance. Although 60% (15 of 25 species included in the analysis) of the species indicated a negative relationship with water hyacinth during winter 2007, the overall relationship was significantly positive. Only about 40% of the species observed (11 of 27 species) had a consistent relationship between abundance and water hyacinth cover between winter 2007 and 2008 (Table 8).

#### Proportional water hyacinth use

Gadwall was the only species that significantly selected for water hyacinth ( $\alpha \leq 0.025$ ;  $n=3$ ), and this only occurred during winter 2007. All other species used water hyacinth within the expected range predicted by daily water hyacinth availability.

Figure 7: The winter 2007 CCA biplot illustrates the relationship between individual species and water hyacinth cover. Species that correspond positively to water hyacinth cover are named, other species are noted with + and sites by Δ. The line represents the magnitude of water hyacinth's effect on community composition.



**Table 8: Final CCA scores for each species during winter 2007 and winter 2008. Positive scores indicate a positive relationship between species abundance and water hyacinth cover. NA indicates the species absence during that season.**

Species	Final CCA scores	
	winter 2008	winter 2007
Double-crested Cormorant	-2.3343	-1.2445
Northern Shoveler	-1.7103	NA
Fulvous Whistling Duck	-1.3342	-3.452243
Common Moorhen	-1.0595	-1.441669
Little Blue Heron	-0.9830	0.451959
Blue-winged Teal	-0.9749	0.167196
Snowy Egret	-0.8322	1.032013
Grebe	-0.7616	-1.923143
Black-crowned Night Heron	-0.6423	0.29628
Cattle Egret	-0.5424	0.589331
American Coot	-0.4420	-0.5272
Great Blue Heron	-0.3597	-0.487722
Tricolored Heron	-0.2986	1.020199
American Pelican	-0.2619	0.907741
Mexican Duck	-0.2488	NA
Great Egret	0.0518	-0.048734
Belted Kingfisher	0.1347	-3.72534
Killdeer	0.1353	-0.412384
Caspian Tern	0.2241	-2.081599
Green Heron	0.3220	0.090544
Northern Jacana	0.9797	9.710649
Black Stilt	1.0778	1.453155
Cinnamon Teal	1.5932	1.006011
Glossy Ibis	2.9711	5.655879
Phalarope	NA	-3.330805
Sandpiper	NA	-1.979857
Common Snipe	NA	-0.067785

## DISCUSSION

### Abundance

I did not find conclusive evidence to support the Intermediate Cover Hypothesis (Figure 2c). The positive relationships between water hyacinth cover and waterbird abundance during fall 2006 and 2007 occurred during seasons of relatively high water hyacinth cover and relatively low mean waterbird abundance. I did not find a significant relationship between waterbird abundance and water hyacinth cover during seasons of high waterbird abundance (e.g. summer 2007, winter 2008, and summer 2008). Perhaps because waterbird abundance at the site level was low (i.e. below site carrying capacity) during both fall seasons more birds could be added to the site with increasing water hyacinth. It is also possible that ecological factors other than water hyacinth cover (e.g. precipitation, temperature, nutrient influx, etc.) influenced the waterbird relationship with water hyacinth, but those factors were beyond the scope of this study. Waterbird abundance was generally higher during summer than other seasons (Figure 4). This is contrary to expectations based on the influx of wintering species and transient (stop-over) species in winter and fall. Greater summer abundance may be explained by the breeding season, but no species observed was exclusive to this season.

While abundance of the four most common waterbird species significantly corresponded to water hyacinth cover at some time during this study, Snowy Egret abundance was positively related to site water hyacinth cover during 3 of 7 study seasons. Patches of water hyacinth are dense and stable enough for birds to stand upon, and thus provide island-like habitat for birds. Furthermore, the edge of water hyacinth mats have been shown to support greater abundance and diversity of fish and invertebrates (Brendonck et al. 2003, Toft et al. 2003), common prey of

wading bird species (Custer and Osborn 1978, Kushlan 1978, Master et al. 2005). Snowy Egrets are among the smaller wading bird species found at Lake Chapala. The Snowy Egret may be utilizing sites with water hyacinth more than other species to reduce competition with larger species like the Great Egret and Great Blue Heron (Roughgarden 1976).

### Species diversity

Winter migratory species may increase species richness but not necessarily increase species diversity. Here I found that the index of diversity was lower when migratory species were included. This suggests low abundance of wintering species, with the exception of the American Pelican that was extremely abundant during winter months. There was a significant positive correspondence between water hyacinth cover and waterbird species diversity with and without migratory species in winter 2008. Mean winter 2008 water hyacinth cover (2.75%) was significantly less than other seasons within the study, except summer 2008; the highest observed cover was 30% during only one site visit. Contrary to my initial expectation and the intermediate cover hypothesis, no ecological threshold for species diversity was found for winter 2007. Therefore, I suggest that the positive correspondence between water hyacinth cover and species diversity in winter 2008 was attributed to factors other than water hyacinth.

### Community composition

The results from the CCA suggest that the relationship between water hyacinth cover and waterbird community composition was strongest during winter 2007. As mentioned, winter

2007 had the highest seasonal average water hyacinth cover. Since I found a significant relationship for this season alone it may suggest a high threshold at which water hyacinth cover alters community composition. In other words, mean water hyacinth cover less than 18% may not be sufficient to deter or attract species. The species that were positively affected (i.e. increased abundance with increased water hyacinth) were not consistent with expectations based on prior habitat use studies. I expected larger wading birds like the Great Egret, Great Blue Heron, and Snowy Egret to be found in greater abundance at sites with abundant water hyacinth because their long legs enable them to forage in deeper water and maneuver through the dense plant structure with little difficulty (Kushlan 1978; 1986). Of the larger wading birds, only Great Egret abundance was positively related to water hyacinth cover. Several small migratory shorebird species, including the Common Snipe, Sandpiper, and Phalarope, were only seen during winter 2008. The addition of these species altered waterbird community composition, but it is not clear whether their arrival was attributed to less water hyacinth, factors not measured in this study (e.g. precipitation), or to low detectability in dense water hyacinth mats. It is possible that the threshold at which water hyacinth begins to affect these particular shorebird species may be considerably lower than other species within the community. This is likely attributable to the exclusion from suitable foraging habitat that occurs when water hyacinth covers a shoreline, even at low percent cover, and could explain their absence in winter 2007.

#### Proportional water hyacinth use

Of all the species during all the seasons of this study, Gadwall was the only species found to select for water hyacinth according to the habitat selection function. Contrary to expectations,

smaller shorebird species like Sandpipers, Common Snipes, and Black-necked Stilts did not avoid sites with water hyacinth. However, it is important to note that Sandpipers and Common Snipes were not observed in winter 2007 when water hyacinth was fairly abundant on the shoreline.

In general, the use of water hyacinth varied by waterbird species. Great Egrets and Great Blue Herons were often observed hunting from water hyacinth. Patches of water hyacinth were used mostly by Great Egrets, Snowy Egrets, and Great Blue Herons. In contrast, American Coots were most frequently associated with shoreline water hyacinth. American Coots were the dominant species foraging within water hyacinth; individuals were observed feeding directly on water hyacinth leaves and pecking for invertebrates. Overall, the results from the proportional use versus availability study were not very informative; however, they were consistent with other results in that an inverse relationship (i.e., avoidance) was not found. I suggest this may be because the proportion limits were too restrictive ( $\alpha = 0.025$ ) for selection or avoidance.

## Conclusion

Freshwater ecosystems are among the most significantly human-altered systems in the world according to the Millennium Ecosystem Assessment (2005). While invasive species are considered by many to be a leading threat to global aquatic biodiversity (Mack et al. 2000), there are several other factors that alone and in concert with the introduction and spread of non-native species contribute to the loss of aquatic species (Suski and Cooke 2007). Determining the indirect versus direct causes of diversity loss can be ambiguous and complex, but it has important implications for management. If the impacts of invasive species are not understood,

we cannot appropriately measure the response of control efforts and management dollars may be wasted (Gurevitch and Padilla 2004).

This study attempted to improve our understanding of water hyacinth effects on waterbirds of Lake Chapala. The effects of water hyacinth on waterbirds were inconsistent within and among the various analyses. Observed impacts on waterbird abundance, diversity, or community composition at the site-level were weak and rarely significant in a statistical context. However, this does not mean that specific species did not experience population-level impacts. Therefore, I recommend species-specific analyses in situations where a species is of special concern (e.g. threatened or endangered).

Herbicides were sprayed to reduce water hyacinth cover on Lake Chapala during the course of this study. Site-level cover of water hyacinth decreased substantially from winter 2007 (mean = 17%; standard error; 2%) to summer 2008 (mean = 0.8%; standard error; 0.2%). The low percent of water hyacinth cover throughout this study, but especially during seasons that followed winter 2007 and subsequent herbicide applications, made it difficult to detect a potential water cover threshold within a given season. The fluidity of the system as a result of water hyacinth's mobility may also have weakened my ability to detect major differences in waterbird abundance, diversity, and community composition at the site level. Some sites experienced a greater variability in water hyacinth cover within a given seasons, whole other sites were consistently covered by water hyacinth. Future analysis should take spatial and temporal water hyacinth variability into account when examining potential relationships between waterbirds and water hyacinth. Furthermore, the lack of prior information on waterbird distributions on Lake Chapala hindered my ability to determine if water hyacinth drove the observed differences in waterbird community composition. In this study, I assumed equal

detectability for all species in all habitats. The decrease in water hyacinth cover may have increased detectability of some smaller waterbird species thereby underestimating species abundance and species diversity. However, given the fact that bird observations were conducted by a single person it is unlikely that species would go completely undetected at all sites during the five seasons prior to detection in winter 2008. In the absence of pre-invasion bird distribution data, the best option is to continue to monitor waterbirds on Lake Chapala to determine whether waterbird abundance and diversity increases during years with less water hyacinth.

Overall, there are often more invasive species entering a system than can be controlled, therefore prioritization is becoming increasingly important to managers, especially in aquatic systems. Understanding the holistic effects of non-native species in a given ecosystem will help prioritize efforts and, hopefully, minimize efforts wasted on controlling species that are not directly responsible for ecological damages. Conducting community-level analyses offers an opportunity to investigate the effects of an invader from a wider perspective that can become more focused (in terms of species and sites) where needed. For Lake Chapala specifically, I recommend continued waterbird monitoring for ‘new’ or returning migratory species that may be responding to less water hyacinth cover.

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## Chapter 3

### **Habitat use and behavioral response of American Coots to an invasive freshwater plant, *Eichhornia crassipes***

**Keywords** American Coots, *Fulica americana*, Behavior, Habitat use, Foraging, Invasive plants

#### **INTRODUCTION**

The effects of invasive plants have been well documented for plankton and fish communities, but little is known about the effects of non-native plants on bird communities (Johnson and Montalbano 1984, Folker 1987, Johnson and Montalbano 1987). Invasive aquatic plants in freshwater and wetland systems can greatly alter the habitat available to waterfowl via increased abundance of invertebrates and forage fish (Watkins et al. 1983), providing an indirect source of food for waterbirds. Like their native counterparts, invasive plants can also provide a food source for waterbirds (Montalbano et al. 1979, O'Meara et al. 1982, Folker 1987). Water hyacinth (*Eichhornia crassipes*), a common invasive aquatic plant found throughout tropical and subtropical areas globally, is recognized as one of the worst invasive species in the world (Center 1994). Studies have shown greater abundance and more invertebrate diversity associated with water hyacinth when compared to other aquatic vegetation and open water (Brendonck et al. 2003, Rocha-Ramirez et al. 2007), yet little is known about how this globally prolific invasive species specifically affects waterbirds (Bartodziej and Weymouth 1995). An increase in waterbird prey abundance and diversity has the potential to support greater waterbird populations and change the distribution of birds within a given area. On the other hand, the physical

attributes of water hyacinth and its distribution along shorelines may impede waterbirds from accessing critical habitat, thus negatively impacting waterbird populations. Understanding how this invasive plant affects particular waterbird species can help us design management plans that better reflect the habitat needs of local species.

American Coots (*Fulica americana*) are among the most abundant resident species at Lake Chapala. According to winter bird counts conducted by the Fish and Wildlife Service, 2789 to 3640 American coots were observed between 2000 and 2006 (USFWS 2000, 2003, 2006). Moreover, American Coots are an appropriate study species because their documented dietary and habitat preferences suggest a potential link with water hyacinth. The majority of the American Coots' diet is thought to be comprised of plant material, including pondweeds, sedges, algae, and grasses (Jones 1940). Animal matter is less common, but include insects, mollusks, arachnids, and crustaceans (Jones 1940, Fitzner et al. 1980, Descrochers and Ankney 1986). American Coots generally feed in shallow water where submerged and emergent vegetation is abundant (Swiderek et al. 1988); this is the same area where water hyacinth clusters in Lake Chapala. The ways in which coots obtain food is important to consider in addition to diet and prey availability. Foraging behavior represents an important aspect of avian survival and species persistence. Considering natural selection pressures, foraging decisions are presumably made to minimize energy expenditure and maximize the quality of resources of obtained. Foraging behavior is tightly linked with the availability, type and quality of food available, and the density of conspecifics (McKnight 1998). Each of these factors is influenced in part by habitat availability and utilization. Therefore, I focused on habitat use and foraging behavior to determine whether water hyacinth is affecting this waterbird species.

Management of Lake Chapala to date has not taken into account the waterbird community or bird use of existing habitat (NGESA 2005). In this study I compare habitat use among sites with varying water hyacinth cover and habitat-associated behavior of American Coots to determine the effects of water hyacinth on waterbirds in this large freshwater system. Behavioral observations help us understand how organisms use the resources available to them (Alcock 1989). The objectives of this study were threefold: to determine whether 1) water hyacinth cover affected overall habitat use by American Coots, 2) behavior of American Coots differed among habitat types, and 3) American Coots foraging habitat selection was influenced by percent water hyacinth cover and, if so, how. An analysis of this type has yet to be conducted for water hyacinth, therefore I expected the results to further our understanding of the effects of invasive aquatic plants, in particular water hyacinth, on the waterbird community and to help account for the waterbird well-being in management decisions (Folker 1987, Johnson and Montalbano 1987).

## **METHODS**

### *Study site*

Lake Chapala is the largest freshwater lake in Mexico covering nearly 112,000 ha (CEA-Jalisco 2008). Located in the central highlands, it is a shallow and turbid lake with high nutrient concentrations (Davalos-Lind and Lind 2001, Lind and Davalos-Lind 2001). Water hyacinth has been present in Lake Chapala, Mexico intermittently for more than 100 years (CEA-Jalisco 2005). Water hyacinth is able to intercept light at the surface and use nutrients in the water column. The lack of light infiltration limits competition from phytoplankton as well as other

shallow-water vegetation (Davalos-Lind and Lind 2001, Lind and Davalos-Lind 2001, Lind and Davalos-Lind 2002). Water hyacinth cover varies around the lake, but at high densities the plant clusters along shorelines, blocking boat access to the lake and sometimes irrigation pipes. It also forms open water mats that drift throughout the lake according to wind and water currents. Water hyacinth control programs in Lake Chapala had been largely unsuccessful until the initiation of a chemical control program first observed in January 2007. In addition to seasonal differences in water hyacinth cover likely attributed to control efforts, lake volume varied among study seasons as well (CEA-Jalisco 2008). Lake levels were extremely low in summer 2007 as a result of a drought and over-extraction of upstream water (CEA-Jalisco 2008). The 2007 rainy season caused the lake to expand and claim much of the surrounding open shore.

**Table 1: American Coot study seasons on Lake Chapala, Mexico.**

Season	Dates
Winter 2007	February 2-23, 2007
Summer 2007	May 24-June 29, 2007
Fall 2007	September 26-October 14, 2007
Winter 2008	January 29-February 22, 2008
Summer 2008	May 28-June 23, 2008

**Table 2: A description of habitat types available and behaviors observed in this study of American Coots at Lake Chapala, Mexico.**

<b>Habitat Types</b>	<b>Behaviors</b>
Open water: water without vegetation	Foraging : dabbling, diving, and directly pecking at substrate and plant material
Patch water hyacinth: water hyacinth mats surrounded by water on all sides	Swimming: movement in water without foraging
Emergent vegetation: rooted vegetation including cattail and bulrush	Walking: movement on land or water hyacinth without foraging
Shoreline water hyacinth: water hyacinth mats clustered along shoreline	Alert: stillness with head posed upward or sudden escape maneuvers
Open shoreline: shoreline without water hyacinth, mainly mud, cobble, and grass	Preening: conspicuous grooming of feathers
Shallow water: water less than 0.5 m deep	Resting: an absence of movement, but without being noticeably alert
Rocks: large above-water rocks	
Submerged trees: stumps and trees surrounded by water; sometimes with foliage.	

*Field methods*

I recorded diurnal behavior of American Coots at 19 randomly selected sites around Lake Chapala during five consecutive seasons (Table 1). I selected individual birds to observe by focusing a 15-60 x spotting scope on a group of coots and choosing the individual at the center-most point within a flock (Altman 1974, McKnight 1998); 1-2 individuals were observed during each site-visit. I monitored each bird for approximately 2 minutes, recording behavior and habitat association every 10 seconds (Table 2). In addition to behavior, I also recorded the

habitat in which the individual was located to estimate habitat use. Habitat availability varied by site around Lake Chapala, but included any combination of eight distinct habitat types (Table 2). I analyzed behavior data by comparing the percentage of time seen within each habitat (Equation 1) and the percentage of time for a given behavior within each habitat (Equation 2).

$$\text{HABITAT USE} = \frac{\text{Time spent in habitat } j \text{ at site } k}{\text{Time observed at site } k} \text{ for flock } n$$

(Equation 1)

$$\text{BEHAVIOR} = \frac{\text{Time spent for behavior } i \text{ in habitat } j \text{ at site } k}{\text{Time observed at site } k} \text{ for flock } n$$

(Equation 2)

I aggregated observations of multiple individuals from the same site-visit (i.e. same site and same day) into a single independent flock record to preserve independence among records (Fasola and Biddau 1997). I used flocks as the basis for all statistical analyses. In addition to the behavioral observations, I counted the number of coots at each site in order to compare species presence (i.e. site-level selection) to the percent water hyacinth cover.

### **Habitat use**

I observed 446 individuals from 220 independent flocks to assess behavior and habitat use among American Coots at Lake Chapala. I calculated habitat use based on the time I

observed coots in each habitat type (Equation 1) throughout the study. I analyzed observed behavior within water hyacinth to detect seasonal shifts in habitat use. I calculated daily water hyacinth cover using aerial photos and on-the-ground estimates for all sites where I observed American Coots and calculated mean seasonal water hyacinth cover for each study season.

### ***Relationships between water hyacinth use and percent cover***

If water hyacinth provided unsuitable habitat for American Coots, one could expect individual birds to either avoid sites with extensive water hyacinth cover or simply avoid water hyacinth within a site by selecting another habitat type. I examined the relationship between the number of coots present at a site and percent water hyacinth cover to test for the first potential response using Kendall's non-parametric correspondence test. I then analyzed the relationship between proportional water hyacinth use and percent water hyacinth cover using the same statistical approach to test for the second response. The Kendall correspondence test is non-parametric and most appropriate for this analysis because a consistent linear transformation could not be found for all seasons of water hyacinth cover data or for proportional use.

### ***Patch versus shoreline water hyacinth use***

I compared the mean time I observed flocks in patch water hyacinth to the time observed in shoreline water hyacinth throughout the study to determine if the location of the plant affected use by coots. I compared the seasonal mean availability of water hyacinth to the proportion of time I observed coots in patch and shoreline water hyacinth combined. I chose to use a

cumulative estimate of percent water hyacinth cover at each site because patch water hyacinth frequently became shoreline water hyacinth during a survey as winds would push it towards shore.

**Behavior-habitat analysis**

I analyzed all five seasons of behavior data together to provide an overview of the range of behavior expressed within different habitat types available around Lake Chapala. By comparing ecologically and spatially related habitat types, I was able to compare water hyacinth directly to the habitat type that would replace it upon removal (Table 3).

**Table 3: Ecologically and spatially related habitat types compared in behavior-habitat analysis of American Coots at Lake Chapala, Mexico.**

Comparison	Habitat types
I	Patch water hyacinth, open water, and emergent vegetation
II	Shoreline water hyacinth, open shoreline, and shallow water
III	Patch and shoreline water hyacinth

I compared the proportion of time spent resting, in locomotion, and foraging among habitat types that were ecologically and spatially related (comparisons I-III). Resting behavior may be an important indicator of stress while resting signifies comfort and security (low stress). Locomotion provides an indicator of energy use as well as simple mobility in certain habitat types. Water hyacinth forms complex and dense clusters that could potentially pose challenges for waterbird mobility, especially smaller species like the American Coots. Foraging behavior is likely the strongest indicator of water hyacinth effects on American Coots because it is closely

linked to habitat type, quality, and prey availability (McKnight 1998). In general, if American Coots were rarely seen foraging in water hyacinth then we might assume that American Coots did not benefit from the enhanced availability of plant material and invertebrates in the system. I tested for seasonal differences in foraging behavior using the same three comparisons described above.

## **Foraging behavior**

### ***Relationship between foraging habitat use and water hyacinth cover***

The composition of foraging habitats may be affected by the percent water hyacinth present at a given site. Based on the results of objective 2, I investigated the impact of water hyacinth cover on foraging patterns using a multivariate approach where the proportion of time spent foraging in various habitats were the response variable and the percent water hyacinth cover at that site the independent variable. This statistical approach tested the possibility that the combination of habitats used by flocks foraging would change as a result of water hyacinth cover. I used a repeated-measures multivariate model (Proc GLM; SAS 9.2) to test for differences in foraging habitat use. I ran the analysis separately for each season.

### ***Seasonal relationship between foraging in water hyacinth and water hyacinth cover***

Based on the results of the multivariate analysis, I continued to investigate seasonal relationships between water hyacinth cover and time spent foraging at a given site using

Kendall's non-parametric test of correspondence. I repeated this analysis for the time spent foraging in water hyacinth. An increase in time spent foraging (energy expenditure) may indicate poor forage quality (i.e. more time is required to obtain enough food). Therefore, the choice to forage in water hyacinth when alternatives are available would suggest that foraging quality is sufficient and water hyacinth potentially preferred.

## RESULTS

### *Study conditions*

All together, 220 flocks (446 individuals) were observed (Table 4). The number of flocks and the number sites at which I observed flocks varied per season.

**Table 4: Distribution and mean time American Coots were observed at Lake Chapala, Mexico from winter 2007 until summer 2008. Flocks are aggregates of all individuals observed during a given site-visit.**

<b>Season</b>	<b>Number of flocks observed</b>	<b>Number of sites where flocks observed</b>	<b>Mean time observed (sec)</b>
Winter 2007	58	19	292
Summer 2007	82	19	257
Fall 2007	4	3	230
Winter 2008	28	17	233
Summer 2008	48	15	124

## **Habitat use**

American Coots were most commonly observed in open water, followed by shallow water, patch water hyacinth, and shoreline water hyacinth (Table 5). American Coots were observed in water hyacinth habitats (shoreline and patch) slightly less than in open water but more than other habitats. American Coots were rarely observed in emergent vegetation; however emergent vegetation was limited within many sites surveyed. In general, open water was the most abundant habitat, except in times of extensive water hyacinth cover at sites located within coves. Water hyacinth frequently accumulated in coves due to wind and currents during winter and summer 2007. Open shoreline varied by season as a function of lake level and water hyacinth cover. Submerged trees were commonly found 5 to 75 meters from shoreline, depending on lake water levels. Although most trees were no longer growing, they provided a substrate for epiphytic algal growth and a structure upon which coots and other waterbirds could roost. I often observed coots tipping down (half-dive) in the shallow-water zone to forage either on benthos or submerged vegetation, although submerged vegetation is not abundant along the shoreline. Rocks were either found along the shoreline or within a meter of the water line. Like submerged trees, rocks provided a structure for coots and other birds, as well as substrate for epiphytic algae.

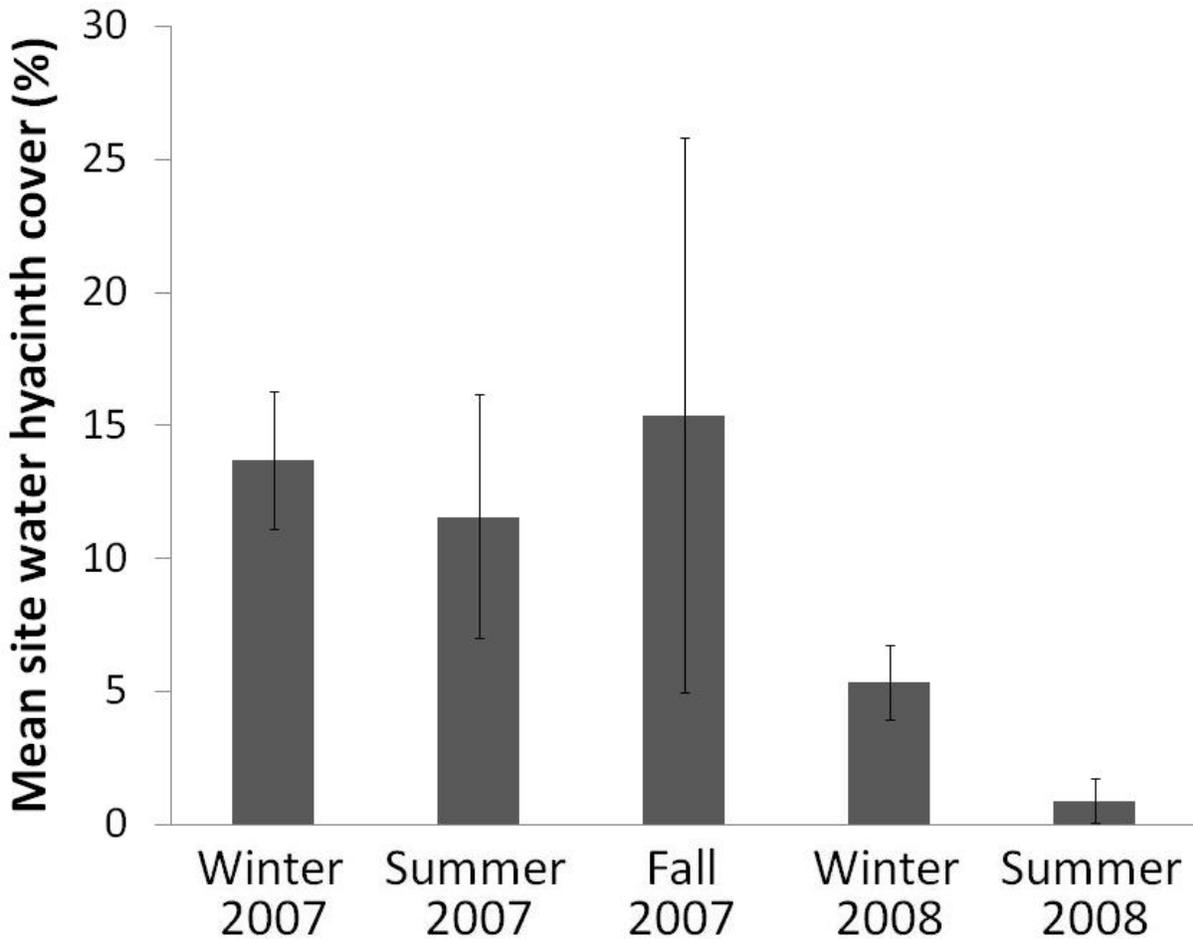
Percent water hyacinth cover varied greatly during this study across seasons as well as within seasons and sites (Figure 1). Within a 24-h period water hyacinth abundance and distribution could change drastically with shifts in wind direction and velocity. American Coots were observed using water hyacinth throughout the study period despite a significant decrease in water hyacinth availability towards the end of the study when mean site cover was less than 1%. Lake level also changed dramatically from season to season (CEA-Jalisco 2008), changing the

availability and location of other habitats. Variability, measured by standard error, in water hyacinth cover was greatest during fall 2007; this was likely attributed to limited flock observations (4 at only three sites).

**Table 5: Total time American Coots were observed in various habitats at Lake Chapala, Mexico from winter 2007 to summer 2008.**

Habitat type	Time observed (minutes)
emergent vegetation	32
open shoreline	74.2
open water	253
patch water hyacinth	123.2
rock	44.5
shallow water	157.3
shoreline water hyacinth	106.5
submerged trees	57

**Figure 1: Mean site cover by water hyacinth on Lake Chapala, Mexico.**



***Relationships between site selection, water hyacinth use, and percent water hyacinth cover***

I did not detect a significant relationship between the total number of American Coots observed at a given site and the percent water hyacinth cover when data from all study seasons were combined ( $n = 409$ ,  $\text{Tau} = 0.0330$ ,  $P = 0.3$ ). The only seasonally significant relationship was during summer 2008; the relationship was negative ( $\text{Tau} = -0.2386$ ;  $P = 0.0019$ ), but water hyacinth was very scarce in the lake during this season (mean < 1%). In contrast, the proportion of individuals observed within water hyacinth was positively related to percent water hyacinth cover within a given site for all seasons except summer 2008.

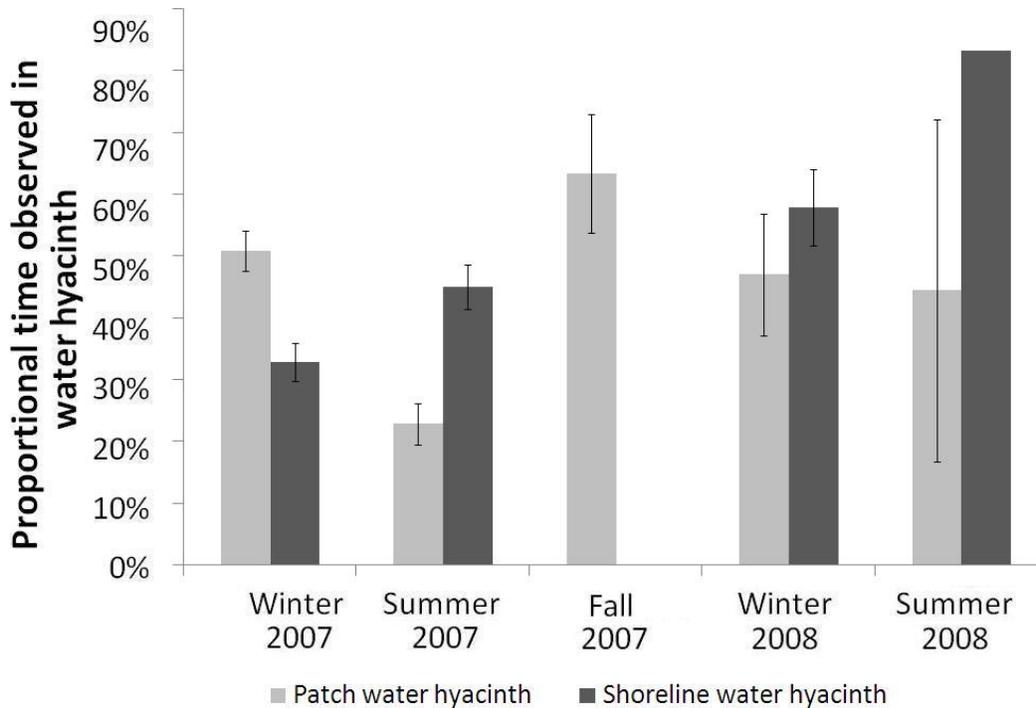
### *Patch versus shoreline water hyacinth use*

The absolute time that American Coots were observed in shoreline and patch water hyacinth varied by season but accounted for more than 30% of total observation time. The time observed in shoreline water hyacinth increased throughout the study, despite seasonal decreases in water hyacinth cover; however, I could not detect a clear seasonal pattern for the time coots were observed in patch water hyacinth (Figure 2). In general, coots were more frequently in shoreline water hyacinth than in patch water hyacinth, except during winter 2007 when mean water hyacinth cover was greatest (Figure 2). The percent of time coots were observed in water hyacinth exceeded the average percent water hyacinth cover for all seasons of this study (Table 6).

**Table 6: Observed behavior within water hyacinth during five study seasons at Lake Chapala, Mexico. Percent water hyacinth cover is the mean seasonal site cover. The percent of total time observed is based on Equation 2. The percent of time behavior *i* observed in water hyacinth is an adjusted percentage for behavior based on the time observed in water hyacinth (time observed for behavior *i* in water hyacinth / time observed in water hyacinth). The percent time observed in water hyacinth is the percent of time American Coots flocks were observed in both patch and shoreline water hyacinth. Percent water hyacinth cover is seasonal mean calculated from sites where American Coots were observed.**

Season	Behavior	Percent of total time observed	Percent of time behavior <i>i</i> observed in water hyacinth	Percent time observed in water hyacinth	Percent water hyacinth cover
Winter 2007	Foraging	29%	68%	44%	17%
	Preening	5%	11%		
	Resting	1%	3%		
	Swimming	7%	17%		
	Walking	1%	2%		
Summer 2007	Alert	<1%	1%	18%	13%
	Foraging	13%	72%		
	Preening	2%	10%		
	Resting	<1%	1%		
	Swimming	2%	12%		
	Walking	1%	4%		
Fall 2007	Foraging	53%	89%	60%	10%
	Swimming	7%	11%		
Winter 2008	Alert	<1%	1%	36%	3%
	Foraging	33%	90%		
	Preening	1%	3%		
	Swimming	2%	6%		
	Walking	0%	0%		
Summer 2008	Foraging	2%	46%	4%	<1%
	Preening	2%	50%		
	Swimming	<1%	4%		

**Figure 2: Mean percentage of time that flocks were observed in patch and shoreline water hyacinth at Lake Chapala, Mexico. Errors bars represent standard error.**



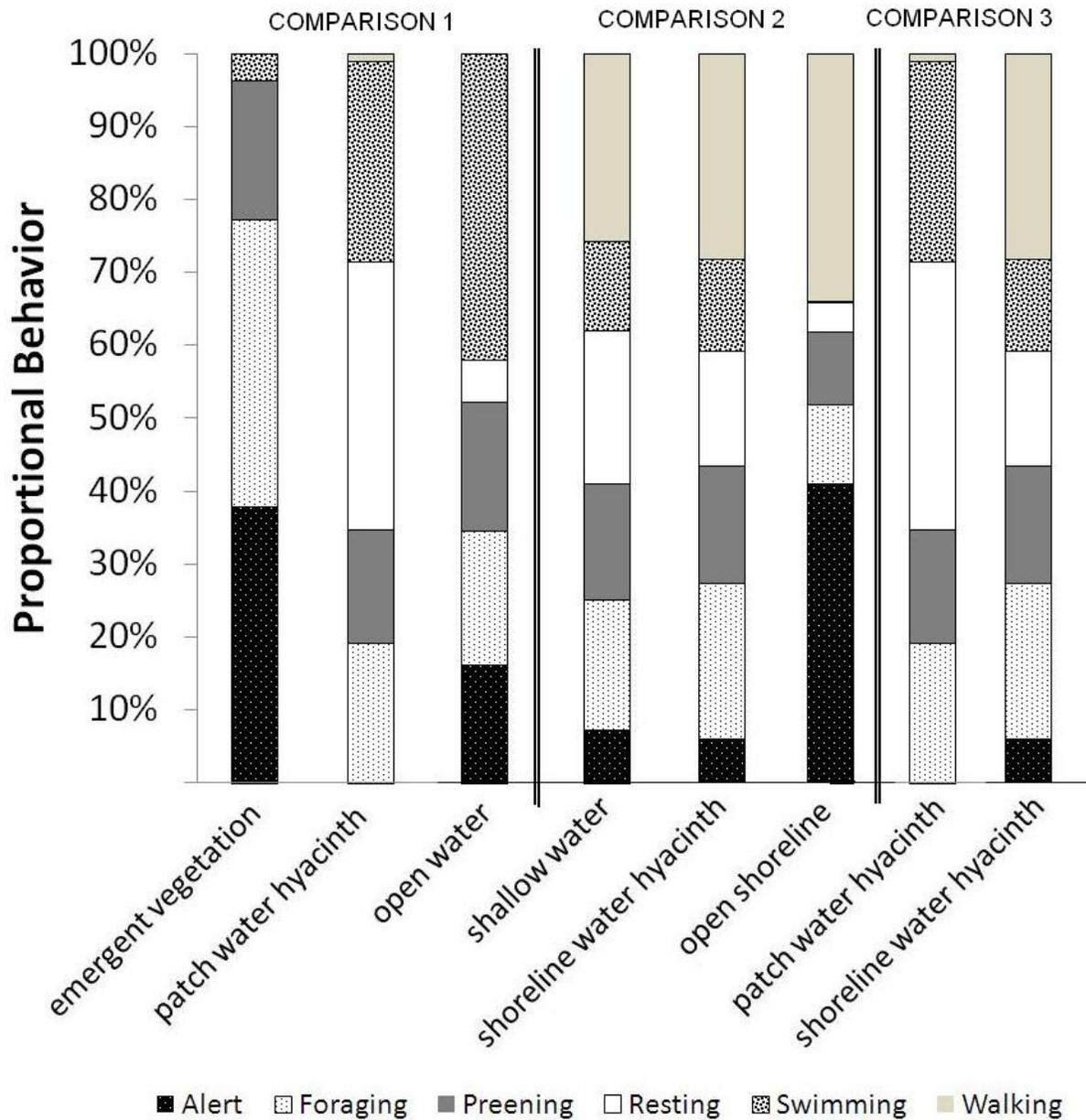
### **Behavior-Habitat Analysis**

#### ***Comparison 1: Patch water hyacinth, emergent vegetation, and open water***

Cumulative behavioral analysis indicated that behavioral patterns varied by habitat type (Figure 3). There was little difference between the proportion of time coots foraged in open water and patch water hyacinth; however, the proportion of time spent foraging in emergent vegetation was less than either of the other two. American Coots spent more time resting in patch water hyacinth than in open water or emergent vegetation. Coots spent more time swimming in open water than through patch water hyacinth, emergent vegetation, or submerged trees. American Coots were alert in emergent vegetation almost 40% of the time observed. In contrast,

American Coots rested on patches water hyacinth more than 30% of the time that they were observed in patch water hyacinth.

**Figure 3: Proportional behavioral patterns (cumulative) of American Coots among habitats at Lake Chapala, Mexico, between winter 2007 and summer 2008.**



### ***Comparison 2: Shoreline water hyacinth, open shoreline, and shallow water***

American Coots spent much less time foraging along open shoreline than in the shallow water, but the time spent foraging in shoreline water hyacinth was only slightly less than shallow water (Figure 3). Along open shorelines, American Coots were observed foraging on epiphytic algae and invertebrates. In shallow waters, typical behavior constituted dabbling and tipping. Foraging behavior along shoreline water hyacinth included biting of water hyacinth leaves or pecking at the root zone, presumably for algae, invertebrates, and root material. Coots were more often observed resting in shallow water areas than in shoreline water hyacinth. Coots walked nearly as much through shoreline water hyacinth as within open shoreline habitat, suggesting water hyacinth did not deter American Coots movement. Coots appeared capable and comfortable walking through even dense shoreline clusters of water hyacinth.

### ***Comparison 3: Patch water hyacinth and shoreline water hyacinth***

There were few differences in American Coot behavior between patch and shoreline water hyacinth (Figure 3). American Coots spent the most time in patch water hyacinth resting, followed by locomotion (swimming) and foraging. American coots spent less time resting in shoreline water hyacinth than in patch water hyacinth but more time was spent foraging. American Coots were rarely alert in shoreline or patch water hyacinth. They spent more time resting in patch water hyacinth than shoreline water hyacinth and more time walking and swimming in association with shoreline water hyacinth. American coots foraging time was fairly equal (approximately 20% of the time in each habitat) between the two types of water hyacinth as well.

## *Seasonal foraging behavior*

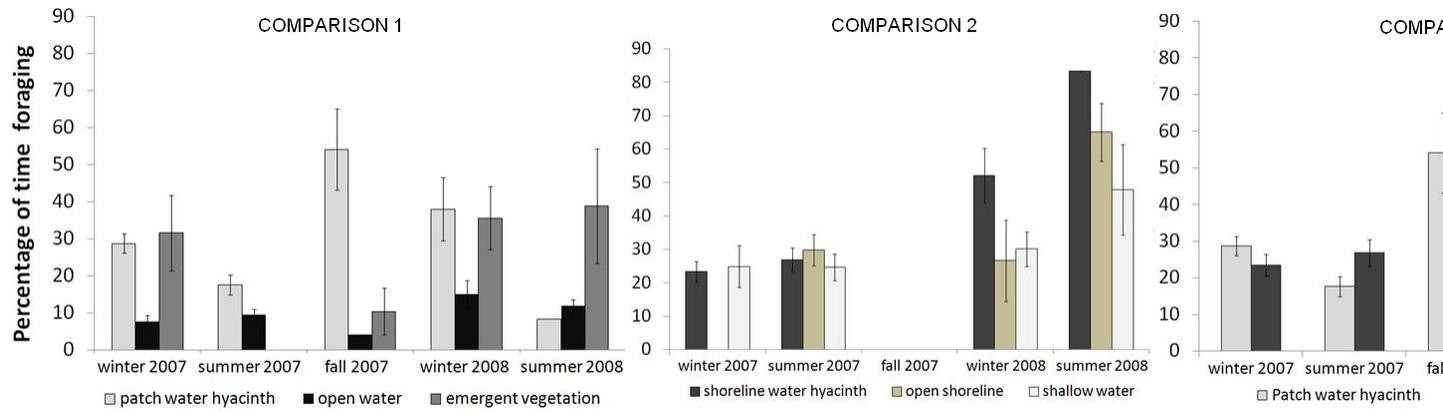
### *Comparison 1: Patch water hyacinth, emergent vegetation, and open water*

One might expect foraging behavior to change throughout the year in response to seasonal changes in prey abundance and habitat availability. American Coots foraged for more time in winter 2007 and 2008 than other seasons, and during those seasons they foraged more in patch water hyacinth and emergent vegetation. American Coots foraged significantly more in patch water hyacinth than in open water for all seasons except summer 2008 (Figure 4, left).

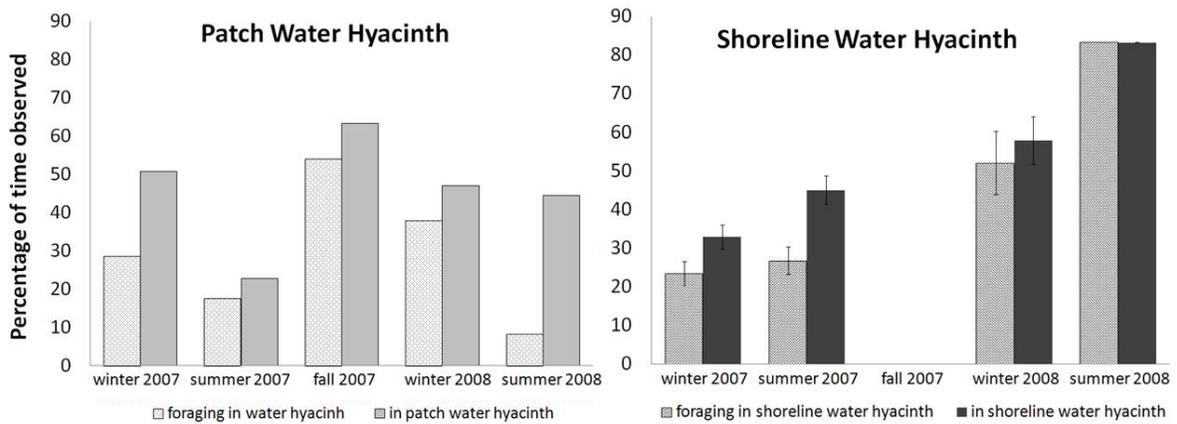
### *Comparison 2: Shoreline water hyacinth, open shoreline, and shallow water*

Interestingly, the percentage of time American Coots foraged in shoreline water hyacinth increased throughout the study despite a drastic decrease in water hyacinth availability. The percentage of time American Coots foraged in shoreline water hyacinth, open shoreline, and shallow waters differed little (Figure 4, middle). Open shoreline was not available during seasons of extensive water hyacinth cover (e.g. winter 2007) yet when it was available, coots frequently pecked on exposed benthic substrate and grass. Both open shoreline and shallow water areas tended to increase during seasons of low lake level, mainly summer 2007. Moreover, foraging along open shoreline area constituted a much greater proportion of time in summer of 2008 when water hyacinth was rarely seen along the shoreline.

**Figure 4: Three comparisons of time spent foraging among habitat types at Lake Chapala, Mexico.**



**Figure 5: Comparison of time spent in water hyacinth to time spent foraging in water hyacinth**



### ***Comparison 3: Patch water hyacinth and shoreline water hyacinth***

There was little difference between the proportion of time I observed coots foraging in shoreline and patch water hyacinth (Figure 4, right). I did not observe American Coots in shoreline water hyacinth during fall 2007 (Figure 5). However, American Coots continued to forage in both patch and shoreline water hyacinth in winter and summer 2008 when water hyacinth cover was less than 4% and 1%, respectively. There was a positive relationship between the time American Coots spent in each water hyacinth habitat and the time they foraged within the same habitat (Figure 5).

### **Foraging behavior**

#### ***Relationship between foraging habitat use and water hyacinth cover***

The combination of habitats used for foraging (i.e. foraging patterns) varied significantly across seasons ( $p = 0.0037$ ) but not with respect to water hyacinth cover. However, water hyacinth cover contributed significantly to observed variability in the foraging patterns on a site-by-site basis ( $p < 0.0001$ ). The relationship between foraging patterns and water hyacinth cover within a given site was significant for all seasons except fall 2007 (Table 7).

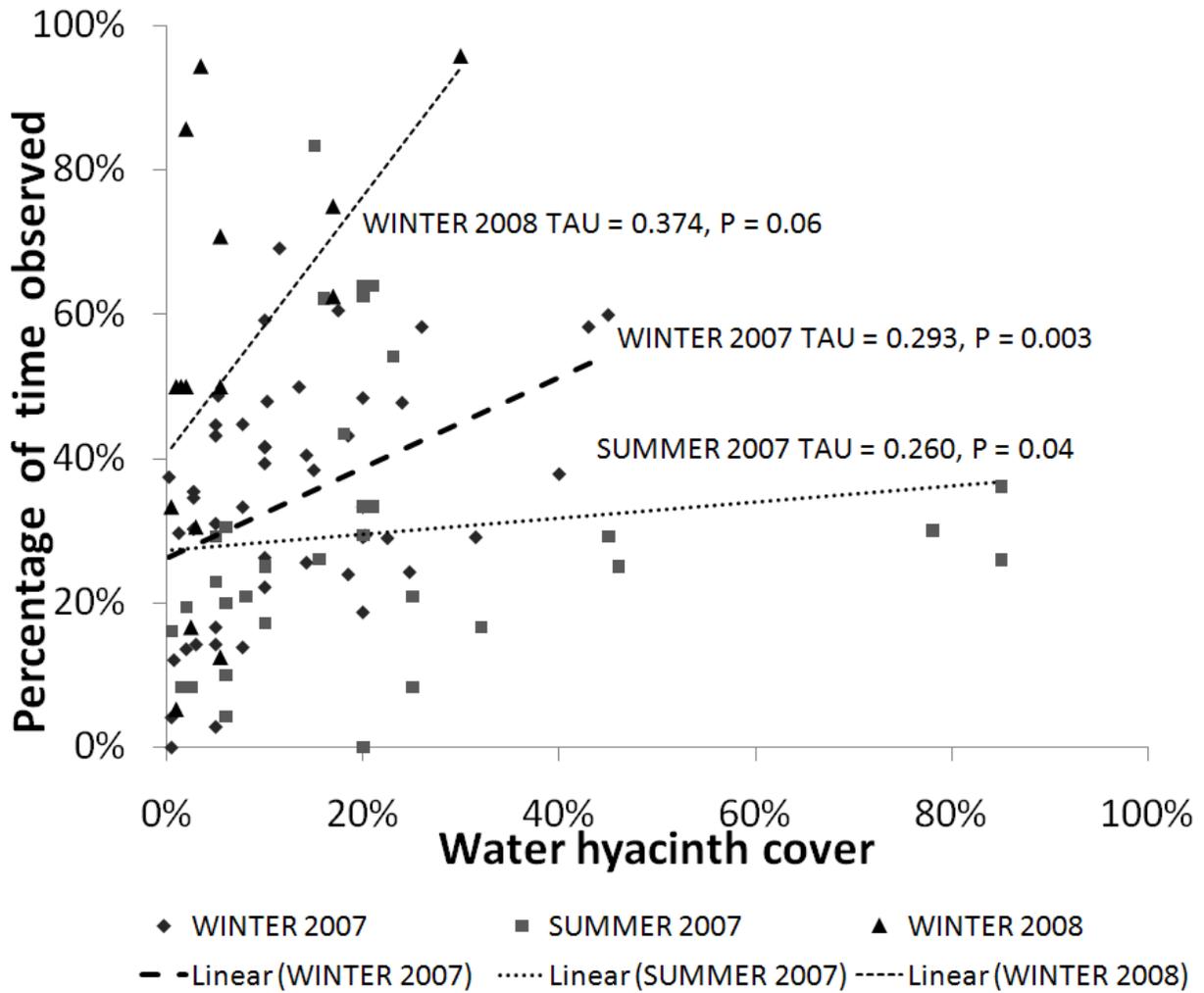
**Table 7: Results (P-values) from the multivariate analysis for the combination of foraging habitats with respect to percent water hyacinth cover on Lake Chapala, Mexico and water hyacinth cover within sites.**

Season	Water hyacinth cover		
	within sites	Water hyacinth cover	Number of sites
Winter 2007	<0.0001	0.83	19
Summer 2007	<0.0001	0.15	17
Fall 2007	0.98	0.58	2
Winter 2008	0.0019	0.25	16
Summer 2008	0.03	0.26	13

*Seasonal relationships between foraging and water hyacinth cover*

I observed 192 (of 220) independent flocks foraging for at least 10 seconds. Based on these flocks, the time that coots foraged at a site was only related to the percent water hyacinth cover during summer 2007 ( $p = 0.0019$ ). Coots spent less time foraging at sites with greater water hyacinth cover during summer 2007. The same was true during winter 2007 and 2008 but the relationships were not significant ( $p = 0.74$  and  $0.71$ , respectively). In contrast, there was a significantly positive relationship between the proportion of time American Coots foraged within water hyacinth at a site and the percent water hyacinth cover at that site for all seasons except summer 2008 (Figure 6).

**Figure 6: Proportion of time that American Coots were observed foraging within water hyacinth in relation to the percent water hyacinth cover at Lake Chapala, Mexico. Tau describes the strength of the relationship between percent time observed and percent water hyacinth. Only the seasons with a significant relationship are plotted.**



## DISCUSSION

This study produced several important results that help us understand the effect of water hyacinth on American Coots of Lake Chapala. Water hyacinth use was fairly consistent throughout the study despite seasonal decreases in water hyacinth availability. The fact that coots were observed more frequently in shoreline water hyacinth during later seasons suggests that American Coots were not excluded from shoreline habitat, despite water hyacinth cover.

American Coots did not appear to avoid sites with water hyacinth, nor did they avoid water hyacinth within a site. In fact, the proportion of time coots were within water hyacinth was higher at sites with greater water hyacinth cover than those with little cover during most seasons. Essentially, the positive relationship between the use and availability of water hyacinth suggests that American Coots used water hyacinth opportunistically and that extensive water hyacinth cover at a given site did not deter site choice. Although I did find a negative relationship during summer 2008, I suspect this was because only one site in the eastern corner of the lake had more than 4% cover during this season; 96 of 108 site-visits had less than 1% water hyacinth cover during summer 2008.

The cumulative behavior analysis supports the non-avoidance conclusion because foraging, swimming, and locomotion occurred in patch and shoreline water hyacinth at least as frequently as in open water or open shoreline. It is interesting to note that foraging in emergent vegetation was not consistent throughout the study. There was an increase in time spent foraging in emergent vegetation during the later seasons when water hyacinth was less available. It is possible that patch water hyacinth may provide a better source of food than emergent vegetation,

but this cannot be proven without sampling potential prey populations (e.g. invertebrate sampling). In contrast to the seasonal variability of foraging within emergent vegetation, foraging in open water was consistently infrequent, despite an increase in available open water with the decrease in water hyacinth cover. This suggests that the loss of open water to water hyacinth patches does not strongly affect food acquisition for the coots. In comparison, the tradeoffs between shoreline water hyacinth and other habitat types within the same zone were much clearer. Foraging in shallow water and open shoreline were affected little by a change in water hyacinth cover during this study, except in summer 2008 when an increase in shoreline, attributed to lower lake levels and to the lack of water hyacinth, clearly affected the foraging strategy of American Coots. Coots foraged in water hyacinth when it was present, suggesting again that they use water hyacinth opportunistically.

The effects of water hyacinth on American Coots were complex and difficult to decipher. This complex relationship is likely attributed to several factors associated with the timing of this study. During the course of this study water hyacinth availability within Lake Chapala decreased drastically, likely due to herbicide water hyacinth control treatments. Lake levels also changed drastically, especially during the summer of 2007 when open shoreline increased by up to 50 meters at some sites. When water hyacinth was present in the lake it was highly mobile, floating across the lake surface by wind and lake currents. Water hyacinth was transitory at some sites but more or less permanent at other sites where dense shoreline clusters developed. In this study, I attempted to tease out potential spatial differences by describing behavior in patch and shoreline water hyacinth separately, but patches of water hyacinth often became part of shoreline water hyacinth cluster. It is interesting that coots continued to use water hyacinth habitats despite low availability in late-study seasons and that there was a positive relationship between time

spent in water hyacinth and time spent foraging in water hyacinth (Figure 5). I believe this further suggests that American Coots used water hyacinth as a food resource (direct and indirect). American Coots seemed less stressed on patches of water hyacinth than in emergent vegetation, resting for more than 30% of the time spent in patch water hyacinth and being alert for 40% of the time in emergent vegetation. Although predation on American Coots at Lake Chapala is not documented, it is possible that patches of water hyacinth provide a refuge for coots from disturbances associated with the shoreline and shallow emergent vegetation areas.

Foraging comprised a large portion of the time that I observed American Coots (47% of the total time observed). One might expect no relationship between percent water hyacinth cover and time spent foraging if water hyacinth and/or associated invertebrates did not represent a major component of the American Coots' diet at Lake Chapala. If foraging in water hyacinth was random or supplemental to other sources, we would not be able to detect a pattern based on percent cover. Moreover, one might expect American Coots to avoid sites with extensive water hyacinth cover that may exclude other habitat types. However, this was not the case at Lake Chapala. All of the analyses conducted in this study suggest that American Coots respond positively to changes in water hyacinth cover (i.e. increases in cover result in more coots in water hyacinth and more time foraging within water hyacinth). In conclusion, I found that American Coots neither avoided water hyacinth habitats or sites with high water hyacinth cover at Lake Chapala. Moreover, I observed American Coots actively foraging within and on water hyacinth, suggesting that it provided suitable forage habitat and prey availability.

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## Chapter 4

### **A question of complexity: effects of water hyacinth (*Eichhornia crassipes*) on aquatic invertebrates of Lake Chapala, Mexico**

**Keywords** Freshwater invertebrates, Zooplankton, *Eichhornia crassipes*, Water hyacinth, Invasive species

#### **Introduction**

Invertebrates are a critical component of the aquatic food web. They provide valuable food resources for other invertebrates (Peckarsky et al., 1990), fish (Guzman-Arroyo, 1995, Lewin et al., 2004), and waterbirds (Bartodziej & Weymouth, 1995). A change in invertebrate assemblages can directly and indirectly affect the rest of the food web, causing ecological and economic change. Aquatic invertebrates are primarily affected by the structure of the macrophyte community (Sharitz & Batzer, 1999, Masifwa et al., 2001b, Meerhoff et al., 2006), turbulence, light intensity, temperature, food availability (Richards et al., 1985, Maceina et al., 1992), and dissolved oxygen (Kiorboe & Saiz, 1995). Changes in vegetation composition can alter the density and composition of predator and prey communities, thus having an indirect effect on invertebrates (Lampert, 1977, Meerhoff et al., 2003, Mangas-Ramirez & Elias-Gutierrez, 2004). There is often a positive correlation between epiphytic macroinvertebrate densities and the surface area of floating aquatic vegetation (Crowder et al., 1982, Schramm et al., 1987). This is due to the increased availability of substrate for algae and bacteria growth (Richards et al., 1985, Maceina et al., 1992).

Water hyacinth is a floating macrophyte that causes ecological and economic changes in tropical and sub-tropical water bodies worldwide (Center, 1994). It is native to South America but is among the world's most widespread invasive aquatic plants and can now be found in over 50 countries on five continents (Bartodziej & Weymouth, 1995, Brendonck et al., 2003, Lu et al., 2007, Martinez Jimenez & Gomez Balandra, 2007). Water hyacinth is prevalent in water bodies where nutrient levels are high due to agricultural runoff, deforestation, and insufficient wastewater treatment (Wilson et al. 2005). Moreover, water hyacinth intercepts light at the water's surface giving it a strong competitive advantage over submerged vegetation and phytoplankton. This is especially the case in turbid water bodies where water clarity is limited (Davalos-Lind & Lind, 2001).

The roots of water hyacinth vary in length and are complex compared to other aquatic plants (Gopal, 1987). As a result, water hyacinth tends to form dense mats of interlocking roots (Mitchell, 1985). These mats are often seen clustered along shorelines or as floating rafts surrounded by open water. Its root structure provides complex and often novel habitat heterogeneity, especially for epiphytic macroinvertebrates like snails, arachnids (Brendonck et al., 2003), and amphipods (Toft et al., 2003, Rocha-Ramirez et al., 2007), that contributes to greater invertebrate diversity than in phytoplankton alone or emergent vegetation (Brendonck et al., 2003, Toft et al., 2003, Mangas-Ramirez & Elias-Gutierrez, 2004). Higher invertebrate diversity is also attributed to the provision of refuge from harsh abiotic conditions and predation pressure and nursery areas for insects, crustaceans, and fish (Wetzel, 1983, Brendonck et al., 2003). From a landscape perspective, invertebrate densities tend to be higher near the open water edge of water hyacinth mats compared to within mats. A study conducted in the Nile River found the highest density of invertebrates to be along the edge of water hyacinth mats

within 6 m of open water (Bailey & Litterick, 1993). A similar study in Lake Victoria found that water hyacinth at the edge of open water supported a more abundant and diverse invertebrate assemblage than rooted emergent vegetation (Masifwa et al., 2001a). Differences in invertebrate assemblages have also been detected between different species of floating macrophytes (Toft et al., 2003), again suggesting that plant structure plays an important role in determining invertebrate density, diversity, and composition.

Prior studies suggest that the invertebrate response to water hyacinth varies by taxonomic group and geographic location. For example, density of calanoid copepods decreased following the mechanical removal of water hyacinth in a Mexican reservoir, while density of cladocerans and cyclopoid copepods did not change (Mangas-Ramirez & Elias-Gutierrez, 2004). Rotifer density was greatest in open water compared to all other vegetated habitats in India (Arora & Mehra, 2003), and in a study conducted in Zimbabwe, microcrustacean taxa were more abundant at littoral sites without water hyacinth than littoral sites with water hyacinth (Brendonck et al., 2003).

In this study, I compared invertebrates associated with water hyacinth to those of open water, emergent vegetation, and submerged trees within Lake Chapala, Mexico to determine the effects of the non-native plant, water hyacinth. Invertebrates constitute more than 50% of dietary consumption for some fish in Lake Chapala. Therefore, the response of invertebrates to water hyacinth is important to the larger ecological impact and subsequent management of water hyacinth. The invertebrate study discussed here was conducted during 4 sampling seasons: winter (February) 2007, summer (June 2007), winter (February) 2008, and summer (June) 2008 and was a component of a broader study of the ecological effects of water hyacinth on Lake Chapala. The specific objectives of this study were to 1) determine whether the density,

taxonomic richness, and assemblage compositions of invertebrates in the water column varied among open water, within water hyacinth mats, and at the edge of water hyacinth mats; 2) determine whether density, taxa richness, and assemblage compositions of invertebrates in the water column varied within different vegetation types (i.e., water hyacinth, emergent vegetation, and submerged trees); 3) determine which invertebrates were influenced by water hyacinth; and 4) compare invertebrate assemblages within the roots of patch and shoreline water hyacinth plants and determine whether plant size (wet mass) was related to invertebrate density.

## **Materials and Methods**

### **Study Site**

Lake Chapala is the largest lake in Mexico, located in the agricultural-dominated Central Highlands and bordered by the states of Jalisco and Michoacán. Lake Chapala is a shallow, tropical lake and is considered eutrophic in terms of nutrient enrichment, yet has low primary productivity due to turbidity (Davalos-Lind & Lind, 2001, Lind & Davalos-Lind, 2001). It covers approximately 112,000 ha with an average depth of approximately 8 m (CEA-Jalisco, 2008). Water hyacinth has existed, intermittently, in Lake Chapala since the early 1900s and, until recent herbicide treatments, control efforts were largely ineffective (CEA-Jalisco, 2005). We selected ten sites randomly around the lake to collect aquatic invertebrates (Table 1). Sites were located randomly along the lake shoreline in areas with some car access. Adjacent land use differed among sites and at some sites changed during the study. Water hyacinth cover varied greatly among sites and throughout the study (Fig. 1). During our study lake volume (and surface

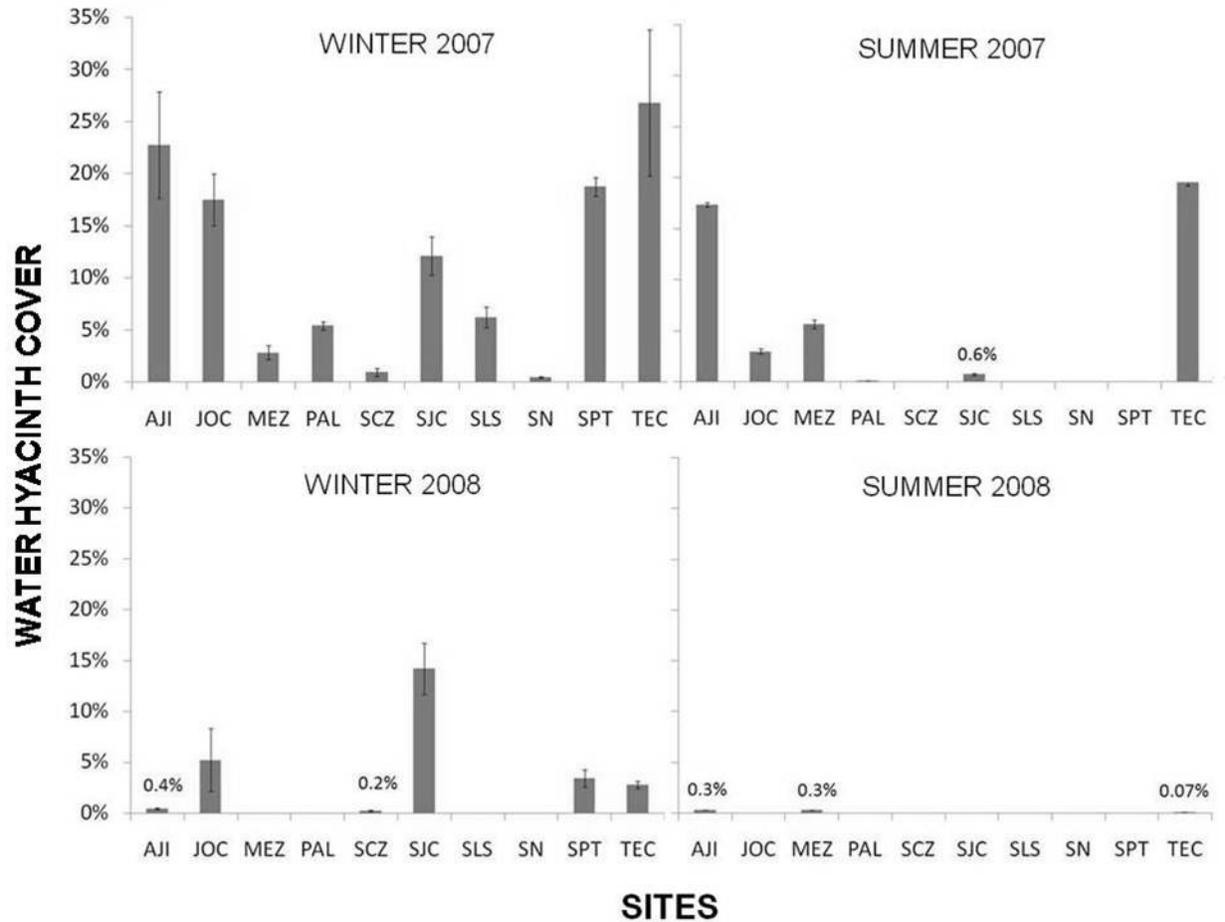
area) also changed drastically as a result of drought and over-allocation of water resources upstream of the lake (CEA-Jalisco, 2008).

**Table 1** Invertebrate sampling sites around Lake Chapala, Mexico.

Site Name	Acronym	Shoreline location	Coordinates (longitude, latitude)	
Ajijic	AJI	NW	20.2959	-103.2620
Jocotepec	JOC	W	20.2837	-103.4138
Mezcala	MEZ	NC	20.3343	-103.0288
San Cristobal Zapótitlan	SCZ	SW	20.2274	-103.3745
San Juan Cósala	SJC	NW	20.2849	-103.3425
San Luis Sóyatlan	SLS	SW	20.1985	-103.3032
San Nicolas	SN	SC	20.1920	-103.2540
San Pedro Tésistan	SPT	SW	20.2311	-103.4121
Palo Alto	PAL	SE	20.1666	-102.9270
Tecómatlan	TEC	NC	20.3234	-103.0995

#### Water hyacinth cover

We calculated water hyacinth cover at these 10 sites around the lake during winter 2007, summer 2007, winter 2008, and summer 2008 to coincide with invertebrate sampling. We used aerial photos and ground surveys to estimate cover. The number of visits per site varied within and among seasons; therefore, we calculated a seasonal mean percent cover for each site, and then calculated an overall seasonal mean by weighting each site equally.



**Fig. 1** Mean water hyacinth cover at ten invertebrate sampling sites around Lake Chapala, Mexico during winter and summer seasons of 2007 and 2008. Bars represent standard error.

### Water column invertebrate sampling

We sampled invertebrates from the top 28 cm of the water column to determine the direct effects of root and plant structure on invertebrates. We collected water from the surface using a 10 cm diameter pvc tube and filtered contents through a 153  $\mu$ m plankton net, rinsing invertebrates into a 250 ml sample jar using 96% ethanol. We sampled invertebrates at sunrise, midday (12:30 in winter and 13:30 in summer), and sunset each day to account for potential

vertical migrations by some species of zooplankton. We collected 3 samples from randomly determined locations of three habitat types: open water, within water hyacinth, and at the edge of water hyacinth. We collected samples from emergent vegetation and submerged trees as well to determine if potential differences were attributed to vegetative structure in general. We determined sample locations using a site grid overlay and a random number table. In areas less than 28 cm deep, we collected water from a maximum allowable depth without touching lake bottom and repeated until we collected approximately 2 liters of water; the shallowest sample was less than 8 cm deep. When the location of water hyacinth changed during a given sampling period, we collected water from areas closest to the pre-designated area that met the habitat type conditions.

We transferred field samples preserved in ethanol into a formalin solution (4%) in order to ship them to the laboratory in the USA. We removed ethanol from samples using a vacuum pump and coarse filter paper, added 4% formalin to sample jars, and stored them until analysis in the lab. We added 4 drops of Eosin Y stain to each sample jar and waited a minimum of 3 hours. We added water to the samples until volume equaled 60 ml to standardize volumes for subsampling. We stirred the sample to create a homogenous solution and took subsamples. Initially, we compared 5 ml (8.3% subsample), 7 ml (11.7%), and 10 ml (16.7%) samples and determined optimal volume to be 2 subsamples of 5 ml without replacement (> 17% of the field sample). When the volume of the sample exceeded 60 ml, we adjusted the subsampling volume to be equal to 17% of the original field sample. We analyzed subsamples under a dissecting scope at 30 x magnification and identified invertebrates to the lowest possible taxonomic group. We analyzed 688 invertebrate samples collected from Lake Chapala; 153 of which were

collected from emergent vegetation and trees (Table 2). All sample densities were standardized to density per liter.

**Table 2** Seasonal sample sizes for invertebrates collected from Lake Chapala during winter and summer 2007 and 2008.

Habitat type	Season	Total number of samples	Samples from water hyacinth	Samples from emergent vegetation & submerged trees
Edge	Winter 2007	70	67	3
	Summer 2007	36	17	19
	Winter 2008	59	14	45
	Summer 2008	12	0	12
Open	Winter 2007	87	-	-
	Summer 2007	96	-	-
	Winter 2008	64	-	-
	Summer 2008	119	-	-
Within	Winter 2007	76	58	18
	Summer 2007	25	4	21
	Winter 2008	28	8	20
	Summer 2008	15	0	15

#### Root invertebrate sampling

We collected water hyacinth plants with fully submerged roots (n=84) from floating patches and shoreline mats during the winter and summer seasons of 2007 and 2008. We weighed wet plants using 600-g and 1000-g spring scales. We then submerged the water hyacinth roots in a bucket of ethanol (96%) and shook the plant vigorously to remove invertebrates. We filtered the ethanol solution containing invertebrates through a 153- $\mu$ m

plankton net and rinsed invertebrates into a sample jar. We then picked off remaining invertebrates using entomological forceps and placed them into the sample jar. We filtered the samples using a vacuum pump and coarse filter paper to remove all the ethanol, preserved samples in 4% formalin and transported them to the laboratory at Virginia Tech where we filtered them through a 0.5-mm mesh. We identified individuals to the lowest taxonomic group possible under a dissecting scope at 10-30x (Pennak, 1953, Voshell, 2002). Low-abundance taxa were grouped by class or phylum for statistical analysis.

## Statistical analyses

### *Water column invertebrates*

The density data were not normally distributed and we could not fit a suitable transformation. Therefore, we used a non-parametric (Kruskal-Wallis) analysis of variance (ANOVA) to test for differences in density among the habitat types: open water, edge of water hyacinth, and within water hyacinth mats (objective 1). We analyzed density separately for each season and for all seasons combined. We conducted multiple comparisons to determine the specific differences for seasons where habitat type was found to be a significant factor. We also tested for differences in density among different vegetation samples for edge and within samples using the Kruskal-Wallis non-parametric approach and conducted multiple comparisons when vegetation type was a significant factor (objective 2).

Taxonomic richness was normally distributed; therefore, we used a parametric mixed model analysis of variance (ANOVA) to test for differences in species richness among the habitat types. The species richness model included season, habitat type, time of day, and the interaction among all three factors. We tested for differences in invertebrate assemblages attributed to season, habitat type, and sampling time of day using a multivariate ANOVA (objective 3). Multivariate techniques are considered robust and tend to work well even when data vectors are not multivariate normally distributed (Johnson, 1998). We compared specific taxa density among different habitat types to explain observed assemblage differences. We ran this analysis for all seasons combined with all vegetation types included and then for all seasons without samples from emergent vegetation or submerged trees to isolate the effect of water hyacinth. We calculated mean density of all taxa identified and determined the 4 dominant invertebrate groups represented in the samples. Finally, we calculated mean sample proportions for all taxa identified (i.e., invertebrate group  $i$  density / total invertebrate density for sample  $n$ ).

#### *Root invertebrates*

We calculated mean root invertebrate density (individuals  $\cdot$  l<sup>-1</sup>) and taxonomic richness for patch and shoreline water hyacinth plants for all four sampling seasons. We only collected two plants during summer 2008 because water hyacinth was extremely rare at sampling sites. We applied a logarithmic transformation to root invertebrate density to adjust for non-normal distribution. We tested for differences in root invertebrate density and taxonomic richness between patch and shoreline water hyacinth and among seasons using a 2-factor analysis of variance (ANOVA). We also tested for a correlation between (log) root invertebrate density and plant mass (wet) and calculated a Pearson coefficient for each relationship. We tested the relationship for all plants together and then for patch and shoreline plants separately.

## Results

### Water hyacinth cover

Water hyacinth cover varied widely among seasons decreasing from winter 2007 to summer 2008 when mean cover was less than 1% at all sites (Fig. 1). At the inception of this study, there were 5 sites with greater than 10% water hyacinth cover. Only two sites exceeded a mean of 10% cover in summer 2007 and this was reduced further in winter 2008, with only 1 site exceeding 10% water hyacinth cover throughout the season. Only two sites (AJI and TEC) located on the northern shore of the lake maintained water hyacinth throughout the entire study period. Sites located within coves of the lake tended to have greater water hyacinth cover on average throughout the study. These sites included JOC, MEZ, and TEC. JOC is located in the eastern corner of the lake; MEZ and TEC are located on the north shore of the lake in cove-like areas.

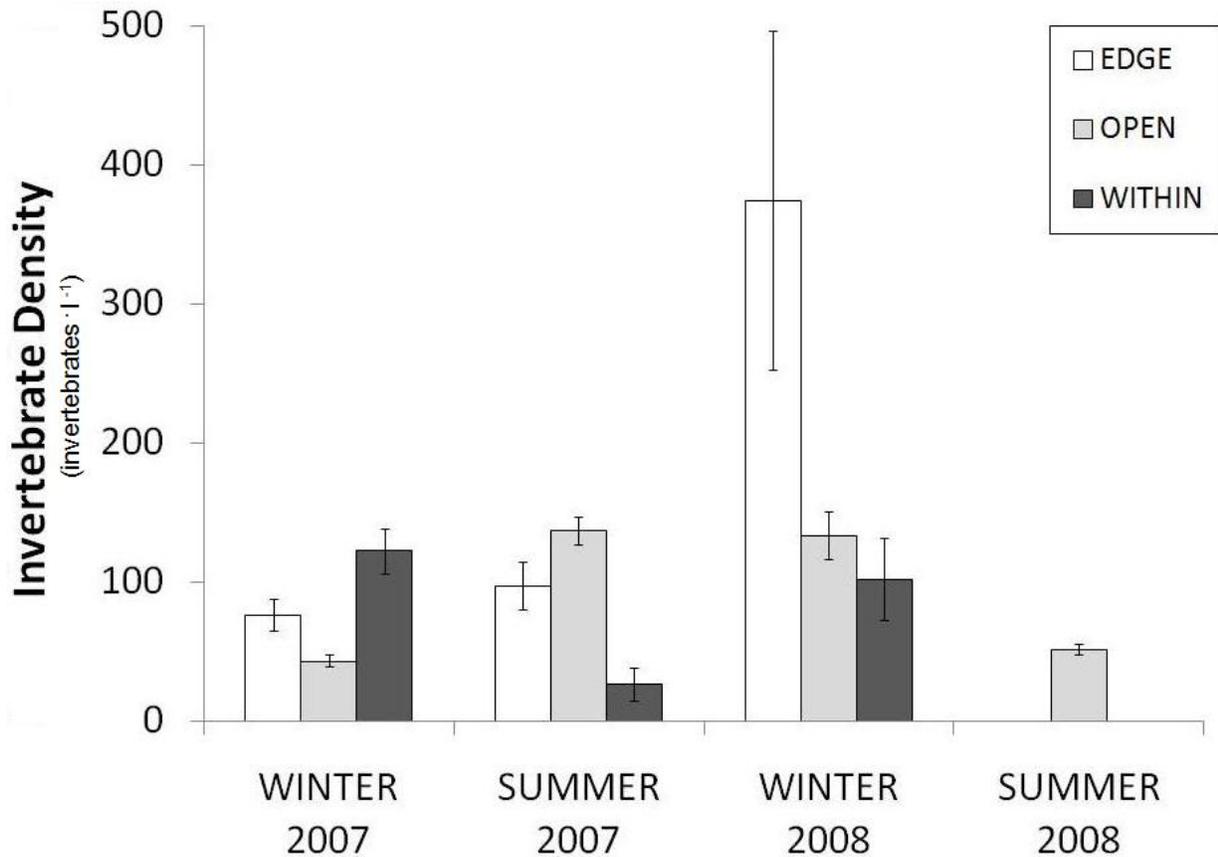
## Invertebrate density within the water column

### *Differences among habitat types*

We identified 15 invertebrate groups throughout this study (Table 3). The mean ranks of invertebrate density differed significantly between open water samples and samples taken from the edge of water hyacinth during winter and summer 2007 (Wilcoxin; winter 2007:  $P = 0.03$ ; summer 2007:  $P = 0.006$ ). Density also differed between open water samples and those taken from within water hyacinth during the same seasons (Wilcoxin; winter 2007:  $P < 0.0001$ ; summer 2007:  $P = 0.02$ ). There was not a significant difference in mean ranks of invertebrate density between samples taken from the edge or from within water hyacinth for any season of this study. Invertebrate density at the edge of water hyacinth was much greater in winter 2008 than other seasons, but this was only based on 14 samples taken during that season and there was not a significant difference among habitat types (Fig. 2). In winter 2007 when water hyacinth cover was most abundant, invertebrate density was greater in water hyacinth than in open water. It is interesting to note that open water invertebrate density was relatively low in summer 2008 when virtually no water hyacinth was present in the lake. While there weren't major differences in invertebrate density across the seasons, the distribution of invertebrates among different habitat types differed by season.

**Table 3** Major taxonomic groups identified in Lake Chapala between February 2007 and June 2008.

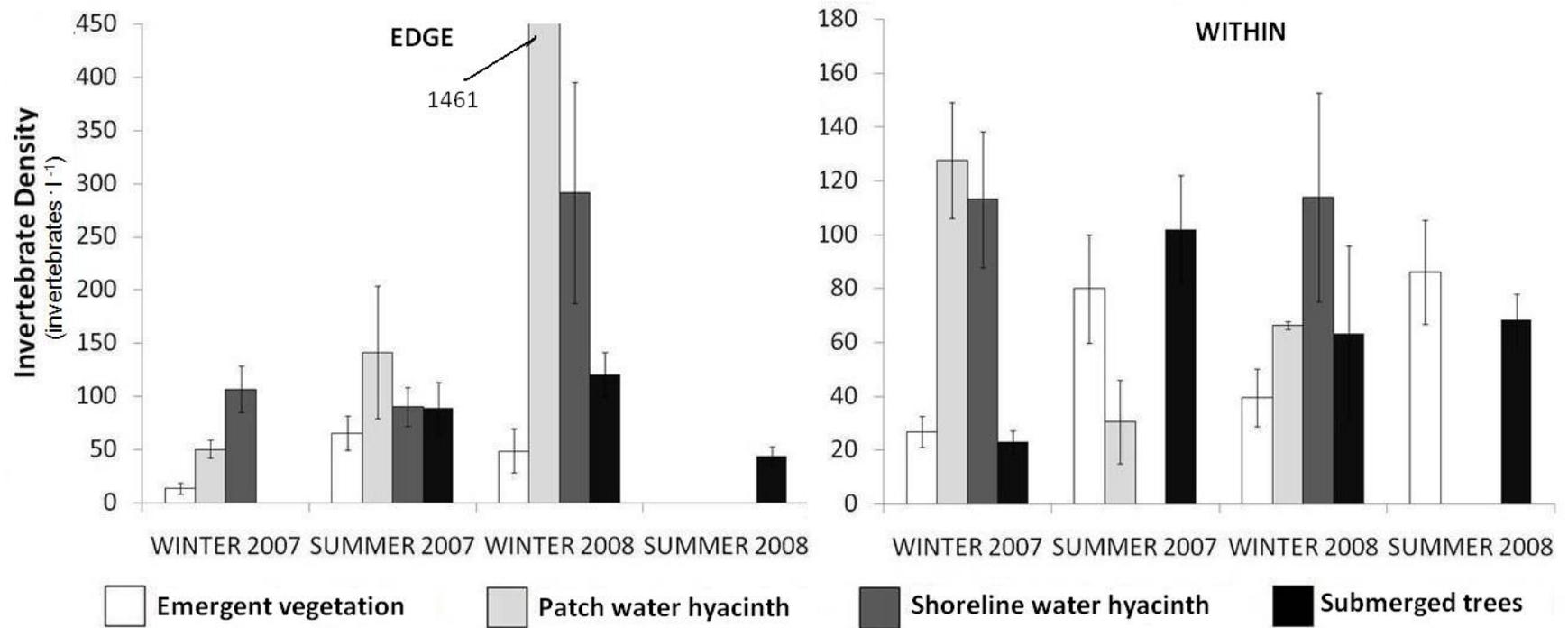
Taxonomic Groups	
Crustacea	Cladocerans
	Copepods (calanoid & cyclopid)
	Ostracods
	Eubranchiopods
	Amphipods
	Decapods
Insecta	Odonata
	Hemiptera
	Coleoptera
	Diptera
	Collembola
Arachnids	-
Annelids	-
Rotifers	-
Gastropods	-



**Fig. 2** Seasonal invertebrate density among habitat types (open water, the edge of water hyacinth, and within water hyacinth) at Lake Chapala. Bars represent standard error.

#### *Differences at the edge of vegetation*

The mean ranks for invertebrate density at the edge of vegetation were significantly different among (vegetation) types during winter 2007 (Wilcoxin;  $P = 0.002$ ) and winter 2008 ( $P = 0.03$ ). Invertebrate density in patch and shoreline water hyacinth was generally higher than in other vegetation types when water hyacinth was available during this study (Fig. 3). In general, invertebrate density was less for all vegetation types at midday. Multiple comparisons revealed a



**Fig. 3** Invertebrate density with respect to vegetation type and season for samples collected from the edge of vegetation (left) and within vegetation (right) at Lake Chapala, Mexico. Bars represent standard error.

higher rank for shoreline water hyacinth than for emergent vegetation in winter 2007, 2008, and for all seasons combined (Table 4).

*Differences within vegetation*

The mean ranks for density within different vegetation types were significantly different among (vegetation) types in winter 2007 (Wilcoxin; P = 0.01). Invertebrate density in shoreline water hyacinth and patch water hyacinth had a higher rank than emergent vegetation during winter 2007. Furthermore, density in patch water hyacinth exceeded density in submerged tree samples in winter 2007 (Table 4). There was no significant difference in mean density rank between patch and shoreline water hyacinth.

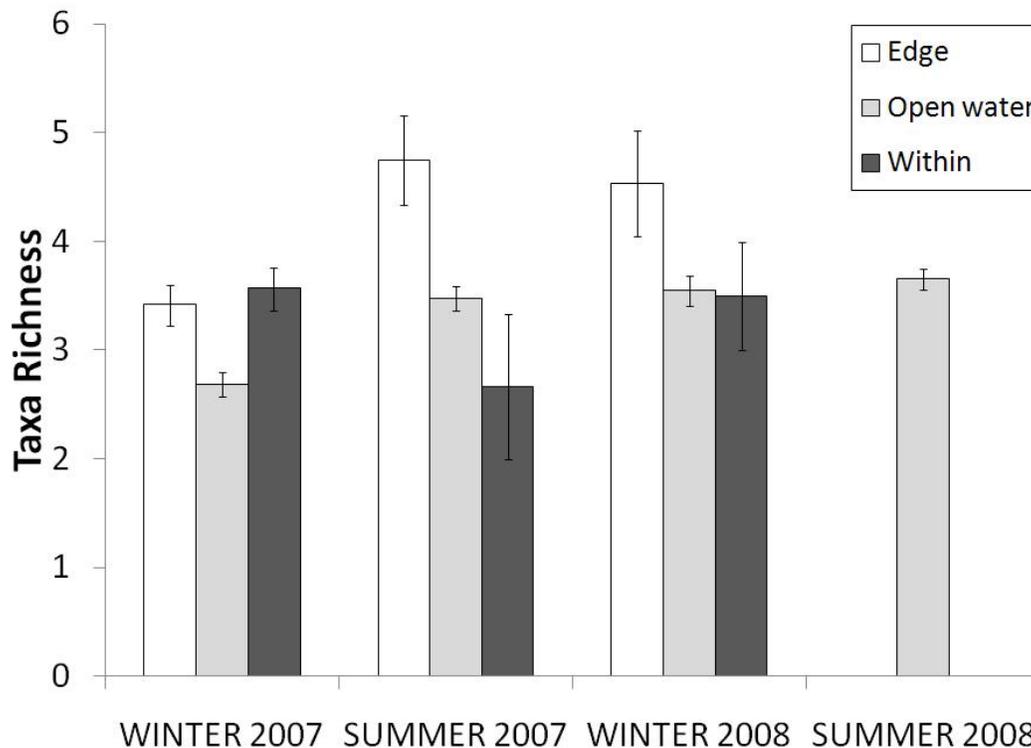
**Table 4** Multiple comparisons (P-values) for significant differences in invertebrate density among vegetation types for samples collected at the edge and within vegetation. Significant differences ( $\alpha < 0.05$ ) are noted in bold. SWH = Shoreline water hyacinth, PWH = Patch water hyacinth, E= Emergent vegetation, and ST= Submerged trees.

Habitat type	Season	SWH PWH	SWH E	PWH E	PWH ST	E ST
EDGE	Winter 2007	<b>0.004</b>	<b>0.01</b>	0.15	NA	NA
	Winter 2008	0.11	<b>0.02</b>	0.12	0.09	<b>0.03</b>
	All Seasons	<b>0.003</b>	<b>0.002</b>	0.57	<b>0.04</b>	<b>0.02</b>
WITHIN	Winter 2007	0.94	<b>0.0006</b>	<b>0.0014</b>	<b>0.002</b>	0.93
	All Seasons	0.79	<b>0.002</b>	<b>0.01</b>	0.12	0.4

## Taxonomic richness within the water column

### *Differences among habitat types*

The most ecologically relevant mixed model with the lowest Akaike Information Criterion (AIC) value for invertebrate taxonomic richness overall included season, habitat type, sampling time, and the 3-way interaction among these factors. Using this model, season and habitat type significantly contributed to the observed variability in taxa richness among samples (ANOVA;  $P = 0.0001$  and  $P < 0.0001$ , respectively), but period alone and the 3-way interaction did not (ANOVA;  $P = 0.327$  and  $P = 0.056$ ). The difference in taxonomic richness among habitat types was less than 2 invertebrate groups on average, implying little difference in terms of richness (Fig. 4). The number of invertebrate groups present in open water samples ranged between 2 and 3 groups throughout the study, and varied less within any given season than the other 2 habitat types. Richness was significantly higher at the edge of water hyacinth than in open water for all seasons for which water hyacinth was present. Edge samples were significantly richer than samples from within water hyacinth during summer 2007 and within samples contained more taxonomic groups than open water in winter 2007. Richness was never significantly higher in open water than in either water hyacinth habitat type.



**Fig. 4** Seasonal invertebrate taxa richness among different habitat types (open water, the edge of water hyacinth, and within water hyacinth) at Lake Chapala, Mexico. Bars represent standard error.

#### *Differences at the edge of vegetation*

Only season and vegetation type contributed significantly to the observed variation in taxonomic richness among invertebrate samples taken at the edge of vegetation (ANOVA;  $P = 0.041$  and  $P < 0.0001$ , respectively). Taxa richness in shoreline water hyacinth differed significantly from emergent vegetation ( $P = 0.008$ ) and patch water hyacinth ( $P = 0.015$ ) in winter 2007. Moreover, taxa richness was significantly greater at the edge of shoreline water hyacinth than submerged trees ( $P < 0.0001$ ) and emergent vegetation ( $P = 0.0004$ ) in summer 2007. In winter 2008, when little water hyacinth was available, samples from the edge of emergent vegetation contained significantly fewer taxa than samples collected from the edge of

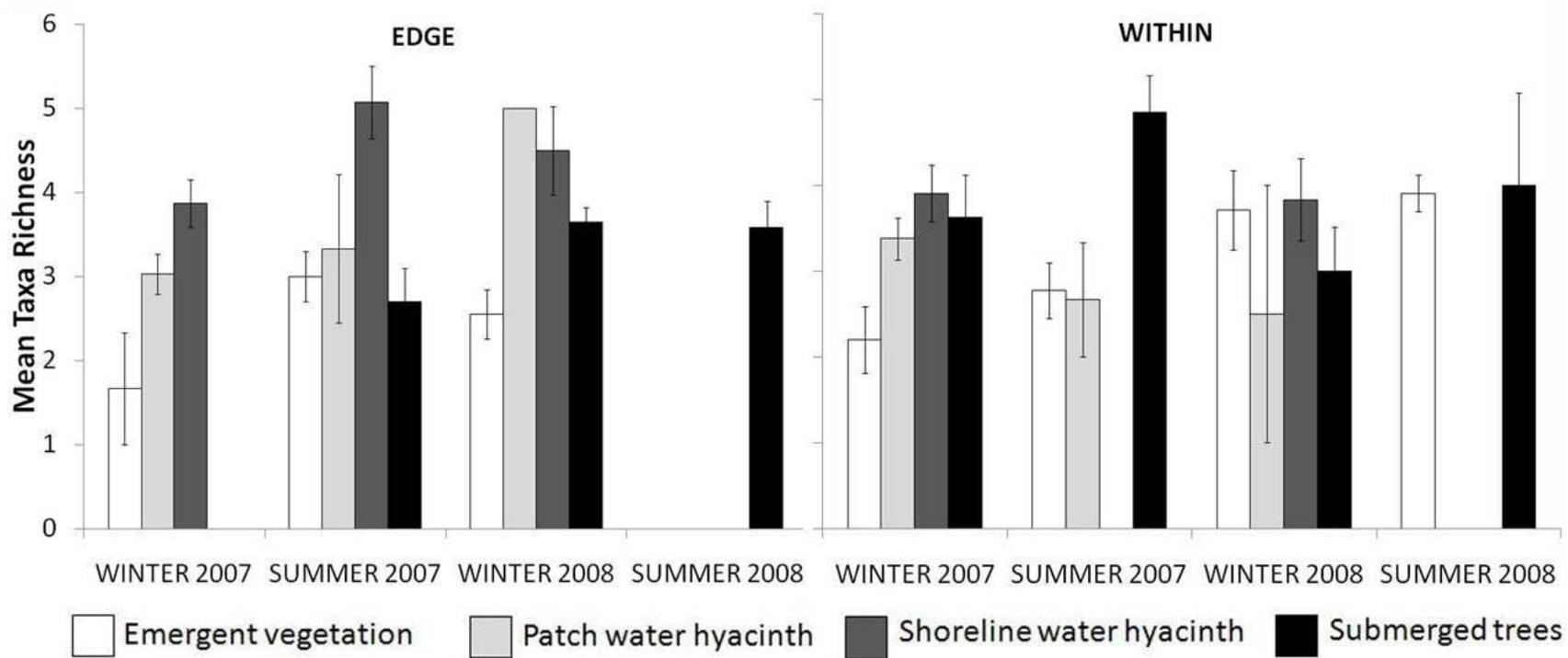
submerged trees ( $P = 0.031$ ) and shoreline water hyacinth ( $P = 0.001$ ) (Fig. 5, left). We only collected samples from the edge of submerged trees in summer 2008 due to the limited availability of water hyacinth.

#### *Differences within vegetation*

The type of vegetation from which samples were collected was the only factor that significantly explained some of the observed variation among taxonomic richness (ANOVA;  $P = 0.015$ ). Taxonomic richness was highly variable from within vegetation samples. We found significantly less richness in samples taken from within emergent vegetation than submerged trees during winter ( $P = 0.049$ ) and summer 2007 ( $P = 0.025$ ). Taxonomic richness was significantly greater within shoreline water hyacinth than emergent vegetation in winter 2007 ( $P = 0.019$ ) (Fig. 5, right).

#### Assemblage composition within the water column

Season, habitat type, and sampling time of day all contributed to observed differences in invertebrate assemblages (MANOVA;  $P < 0.0001$ ,  $P < 0.0001$ , and  $P = 0.002$ , respectively). Contrasts among habitat types revealed significant differences between samples taken from the edge of vegetation (all types) and open water for 8 taxonomic groups (of 13); arachnids and Odonata (Insecta) were not included in this analysis because they were very rare. Similarly, 5 invertebrate groups differed in density between open-water and within-vegetation samples. Nine



**Fig. 5** Invertebrate taxa richness with respect to vegetation type and season for samples collected from the edge of vegetation (left) and from within (right) vegetation at Lake Chapala, Mexico. Bars represent standard error.

invertebrate groups differed significantly in density between samples from the edge of water hyacinth and open water, and 6 groups differed between open-water and within-water hyacinth samples. Significant differences were evident for eubranchiopods (fairy shrimp) and gastropods between edge and within samples for vegetation (all types) and water hyacinth (Table 5). Copepods, rotifers, fairy shrimp, annelids, Diptera larvae, and Collembola were among the groups for which density differed significantly between open water and both forms of water hyacinth habitat types.

Our analysis of invertebrate assemblages among habitat types focuses on differences within a given season and differences over time with changes in seasonal water hyacinth cover by comparing proportional density of invertebrate groups. We did not collect samples from the edge or within water hyacinth during summer 2008, therefore our within-season analysis is limited to winter and summer 2007 and winter 2008.

In the first sampling season (winter 2007), there was little difference in assemblages at the edge or within water hyacinth, with copepods representing an average of greater than 60% of the assemblage within a single sample (Table 6). Cladocerans represented a similar proportion in edge and within samples as well. Cladocerans and rotifers comprised a larger proportion of the invertebrate assemblage in open-water samples than either edge or within samples. Seasonal mean water hyacinth cover at samples sites was 11.4%, the highest of all sampling seasons.

**Table 5** Taxa-specific comparisons among habitat types for all vegetation types together and for water hyacinth. “X” denotes a significant ( $\alpha = 0.05$ ) difference between habitat types.

Taxonomic Group	Significant Differences					
	Edge and Open		Within and Open		Edge and Within	
	All Vegetation	Water Hyacinth	All Vegetation	Water Hyacinth	All Vegetation	Water Hyacinth
Cladocerans	X		X			
Copepods	X	X		X		
Ostracods						
Eubranchiopods	X	X	X	X		X
Amphipods						
Decapods						
Hemiptera		X				
Coleoptera		X				
Diptera	X	X	X	X		
Collembola	X	X	X	X		
Annelids	X	X	X	X		
Rotifers	X	X		X		
Gastropods	X	X			X	X

There were noticeable differences in assemblage composition from winter to summer 2007 and the density of water hyacinth cover decreased from 11.4 to 4.6% mean site cover. A greater proportion of copepods were within water hyacinth than at the edge or in open-water. The proportion of cladocerans within water hyacinth decreased from 23.6% in February 2007 to 12.4% in June 2007. It is interesting to note that, together, the proportion of cladocerans and copepods did not vary much between seasons within water hyacinth, while the cumulative proportion did decrease at the edge of water hyacinth and increased slightly in open water

samples. Other non-dominant taxa comprised 26.6% of invertebrates found at the edge of water hyacinth in summer 2007 that was larger than in any other season or other habitat type.

**Table 6** Proportional density of invertebrate groups at the edge of water hyacinth, open water, and within water hyacinth.

Season	Habitat type	Proportional Density (%)					
		Gastropoda	Eubranchiopoda	Rotifera	Copepoda	Cladocera	Other
Winter 2007	Edge	0.4	2.6	3.2	61.2	25.6	7.0
	Open	0	0.7	9.1	44.3	36.7	9.2
	Within	0	1.3	0.6	64.7	23.6	9.8
Summer 2007	Edge	0.4	6.4	0.3	41.3	25.0	26.6
	Open	0.1	1.7	3.0	56.5	33.8	5.0
	Within	0	0	1.4	73.6	12.4	12.6
Winter 2008	Edge	1.0	2.1	3.5	68.8	19.2	5.4
	Open	0	0	17.4	49.4	23.8	9.5
	Within	0	2.8	3.2	76.1	11.1	6.7
Summer 2008	Edge	0	0	0	0	0	0
	Open	0	0	19.7	57.2	16.4	6.7
	Within	0	0	0	0	0	0

In winter 2008 copepods dominated all three habitat samples. There was little variation in assemblages among habitat types, except for a larger proportion of copepods within and at the edge of water hyacinth and the absence of Eubranchiopoda from open water samples. Rotifera also comprised a much larger proportion of the open water assemblage in winter 2008 than in any other season or habitat type.

Season and vegetation type contributed significantly to variation in assemblages at the edge of vegetation ( $P < 0001$  for both factors); however, sampling time was not significant ( $P =$

096). Cladocerans and copepods varied the most with respect to vegetation type, but there was no significant difference in densities between patch and shoreline water hyacinth (Table 7). Other notable taxonomic groups that expressed significant variation were rotifers, annelids, and Collembola. A significant difference in density existed between patch and shoreline water hyacinth for annelids only. Five taxonomic groups expressed a significant difference in invertebrate density between shoreline water hyacinth and submerged trees, and a different combination of 5 invertebrate groups significantly differed between shoreline water hyacinth and emergent vegetation.

There was less variation in taxa density among samples taken within different vegetation types. Season and vegetation type were again significant factors in explaining observed variation in assemblages ( $P < 0001$  and  $P = 002$ ). The taxonomic group most sensitive to differences in vegetation type was Copepoda, expressing significant differences for all major comparisons except between patch and shoreline water hyacinth. Gastropoda was the only group to express a significant difference between patch and shoreline water hyacinth (Table 7).

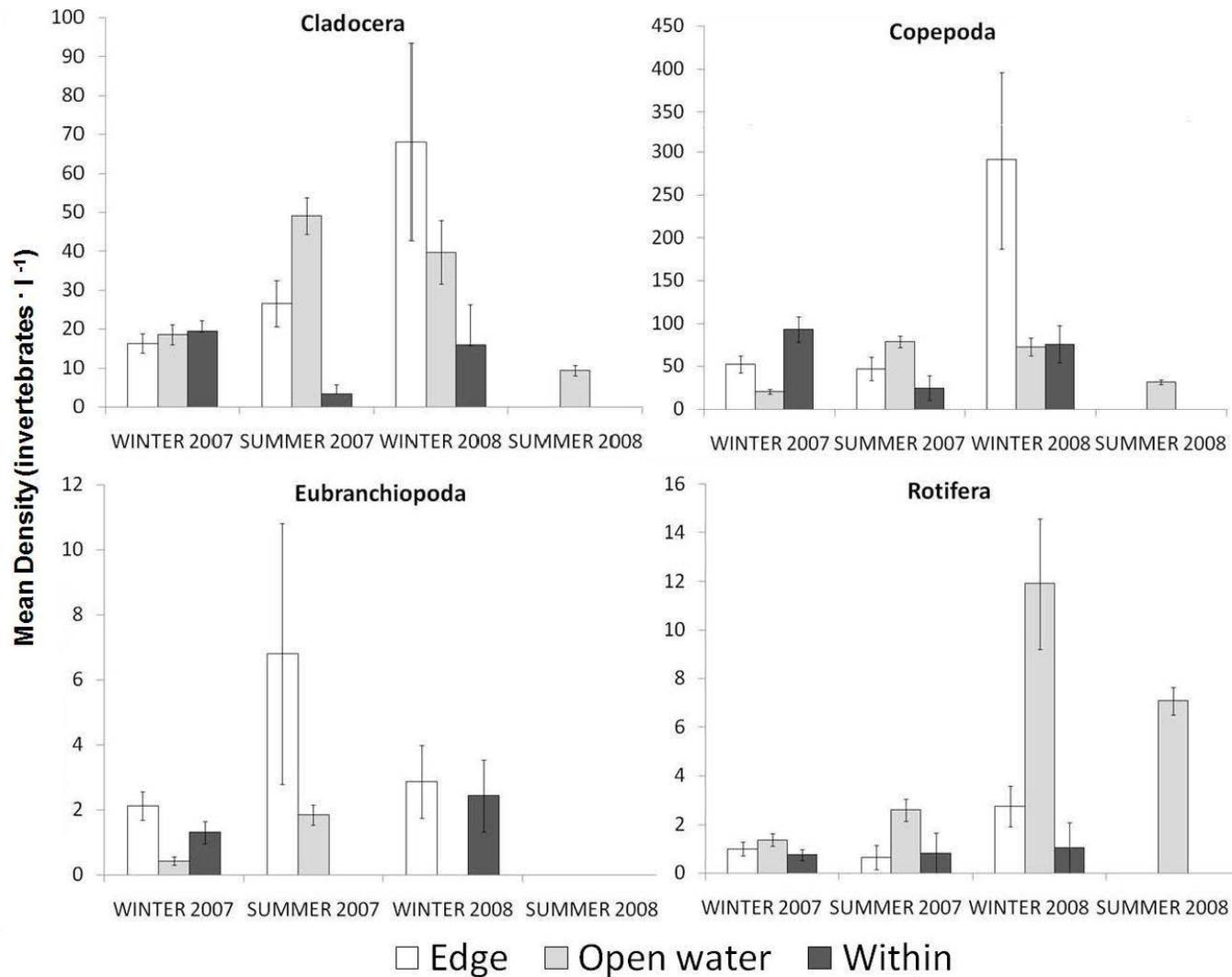
#### *Taxa-specific responses*

Mean water hyacinth cover decreased at all sites from winter 2007 until summer 2008 during our study. Less than 0.5% of water hyacinth cover was observed at any site in summer 2008. We calculated the mean density of the 4 most abundant invertebrate groups (Fig. 6) and three non-dominant groups important to fishes of Lake Chapala (Fig. 7) to investigate densities differences with respect to habitat type and seasonal water hyacinth cover. There was little difference among habitat types for cladocerans and rotifers during winter 2007, when water hyacinth was most abundant. Cladoceran density was greater in summer 2007 and winter 2008

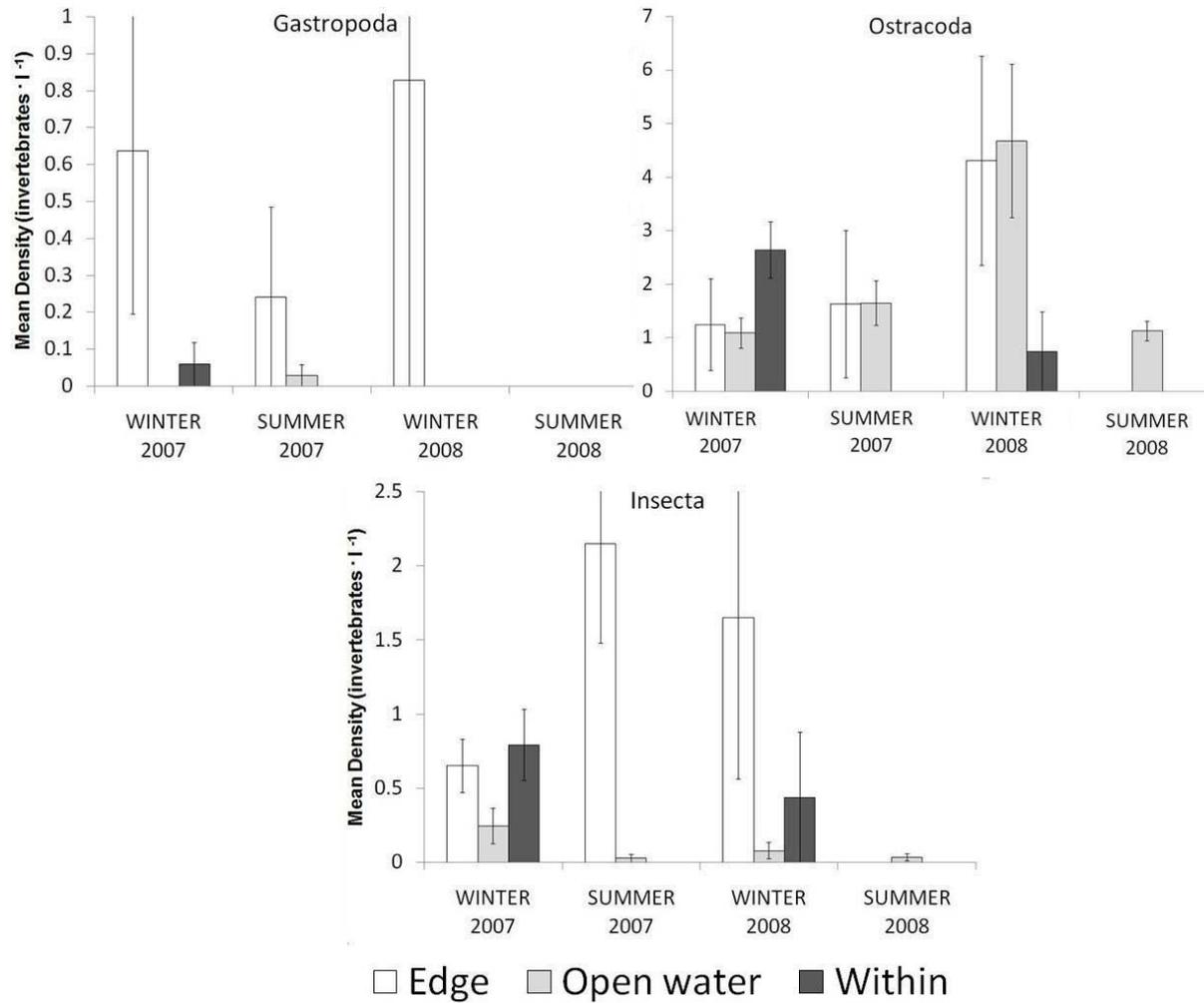
when water hyacinth cover was comparatively low, Moreover, cladocerans were less abundant in samples taken from open water in summer 2008, when water hyacinth as limited, than winter 2008.. Copepod density did not vary much throughout the study, with the exception of the spike for edge samples in winter 2008. A similar density spike was observed for cladocerans and rotifers during winter 2008. We attribute the high variability associated with water hyacinth edge samples to small sample size, but small sample size was not a factor contributing to the observed density spike for rotifers in winter 2008. Rotifers were more common in open-water samples throughout the study, and density in open water was greater in winter and summer 2008 when mean water hyacinth cover was minimal. In contrast, we mostly collected Eubranchiopoda in open water during the first two seasons but only at the edge of and within water hyacinth in winter 2008. Three of the 4 dominant taxonomic groups were least abundant in summer 2008 when water hyacinth was virtually non-existent.

**Table 7** Taxa-specific comparisons among vegetation types. “X” denotes a significant ( $\alpha = 05$ ) difference between habitat types. E= Emergent vegetation, PWH = Patch water hyacinth, SWH = Shoreline water hyacinth, and ST = Submerged trees.

Taxonomic Group	Significant Difference									
	Edge of vegetation					Within Vegetation				
	E & PWH	E & SWH	PWH & SWH	ST & PWH	ST & SWH	E & PWH	E & SWH	PWH & SWH	ST & PWH	ST & SWH
Cladocera	X	X		X	X					
Copepoda	X	X		X	X	X	X		X	X
Rotifer	X	X								
Ostracoda										
Eubranchiopoda					X				X	X
Hemiptera					X					
Coleoptera										
Gastropoda								X		
Annelida		X	X							
Amphipoda										
Decapoda										
Diptera									X	
Collembola	X	X			X					X



**Fig. 6** Mean density of dominant invertebrate groups throughout this study on Lake Chapala, Mexico. Edge = edge of water hyacinth, Open = open water, and Within = within water hyacinth. Bars represent standard error.



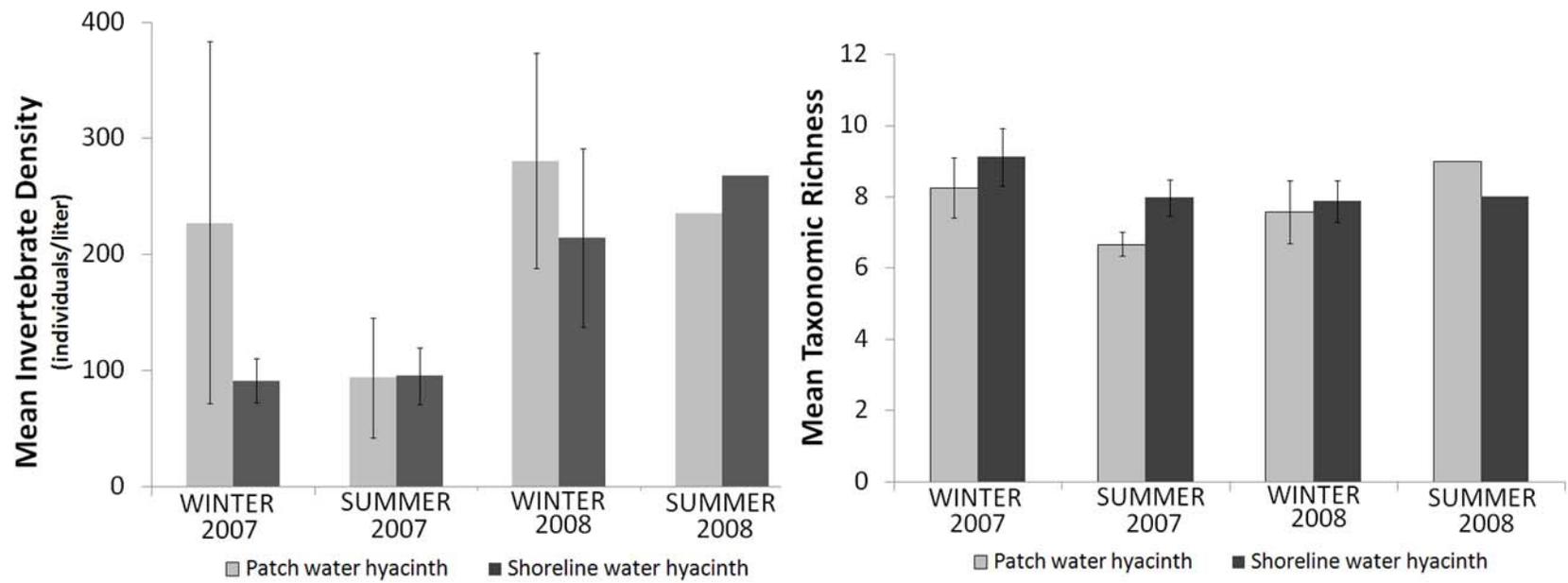
**Fig. 7** Mean density of three invertebrate taxa potentially important to the fishes of Lake Chapala, Mexico based on prior dietary studies (Guzman-Arroyo, 1995). Edge = edge of water hyacinth, Open = open water, and Within = within water hyacinth. Bars represent standard error.

## Root invertebrates

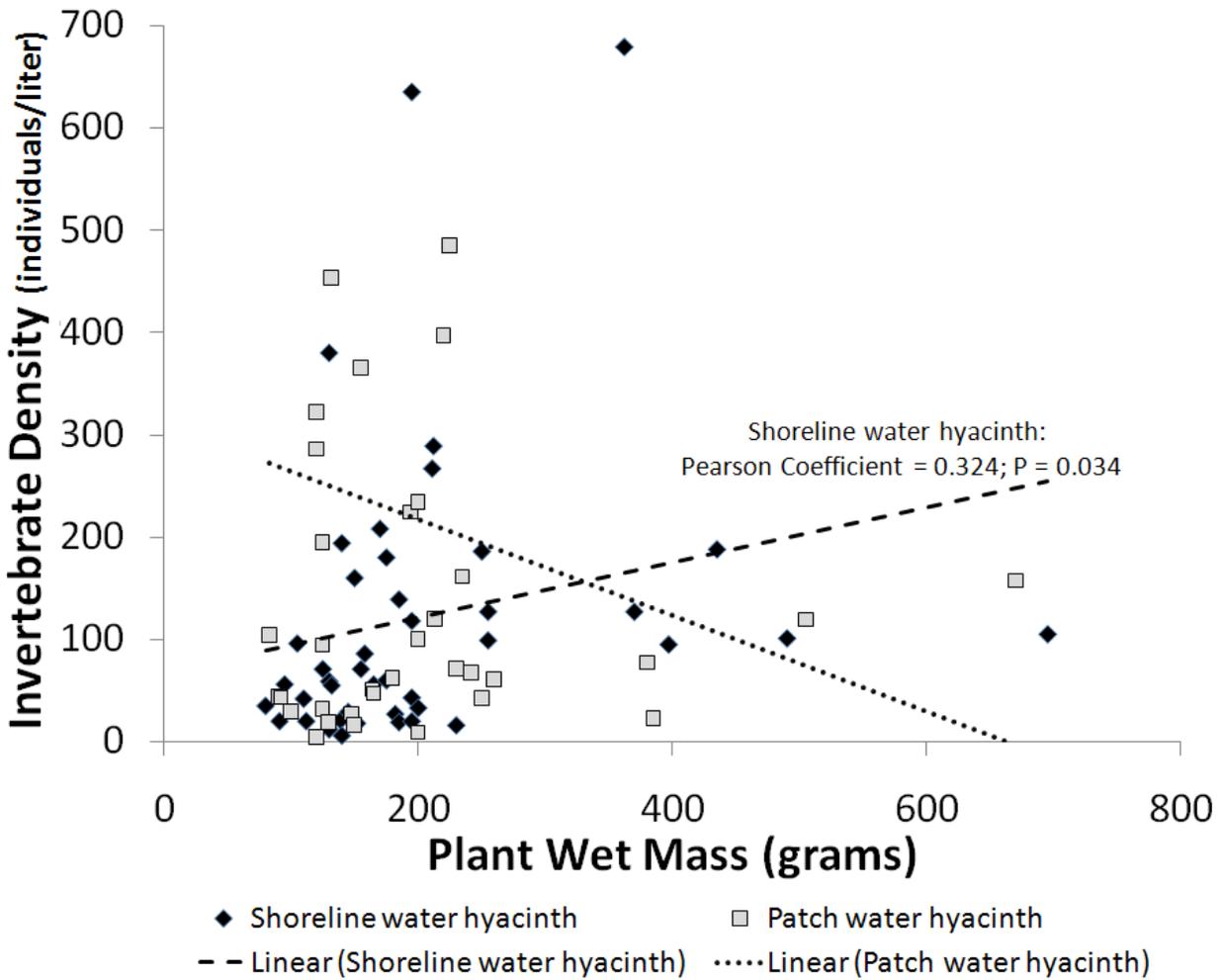
We identified 24 groups of invertebrates within water hyacinth roots (Table 8). There was not a significant difference in total root invertebrate density between patch and shoreline water hyacinth or among seasons ( $P = 0.931$  and  $P = 0.057$ , respectively; Fig. 8 left). Moreover, there was no difference in taxonomic richness between the two types of water hyacinth or among seasons ( $P = 0.352$  and  $P = 0.537$ , respectively; Fig. 8 right). Taxonomic richness remained fairly consistent throughout the study, despite decreased water hyacinth coverage in later seasons (Fig. 1). In contrast, root invertebrate density was greater within the roots during winter and summer 2008 when mean water hyacinth coverage was less than 3%. We found a significant positive correlation between plant mass and total root invertebrate density for shoreline water hyacinth (Pearson coefficient = 0.324;  $P = 0.034$ ; Fig. 9), but this relationship was not significant for patch water hyacinth.

**Table 8** Invertebrate groups identified within roots of water hyacinth at Lake Chapala, Mexico.

Invertebrate groups	
Malacostraca (class)	Isopoda Amphipoda
Arachnida (class)	Hydracarina
Insecta (class)	Diptera Coleoptera Collembola Ephemeroptera Neuroptera Odonata Trichoptera Hemiptera Hymenoptera Plecoptera
Crustacea (class)	Cladocera Copepoda Ostracoda Eubranchiopoda
Bivalvia (class)	-
Gastropoda (class)	-
Oligochaeta (class)	-
Hirudinea (class)	-
Turbellaria (phylum)	-
Hydrozoa (phylum)	-
Nematoda (phylum)	-

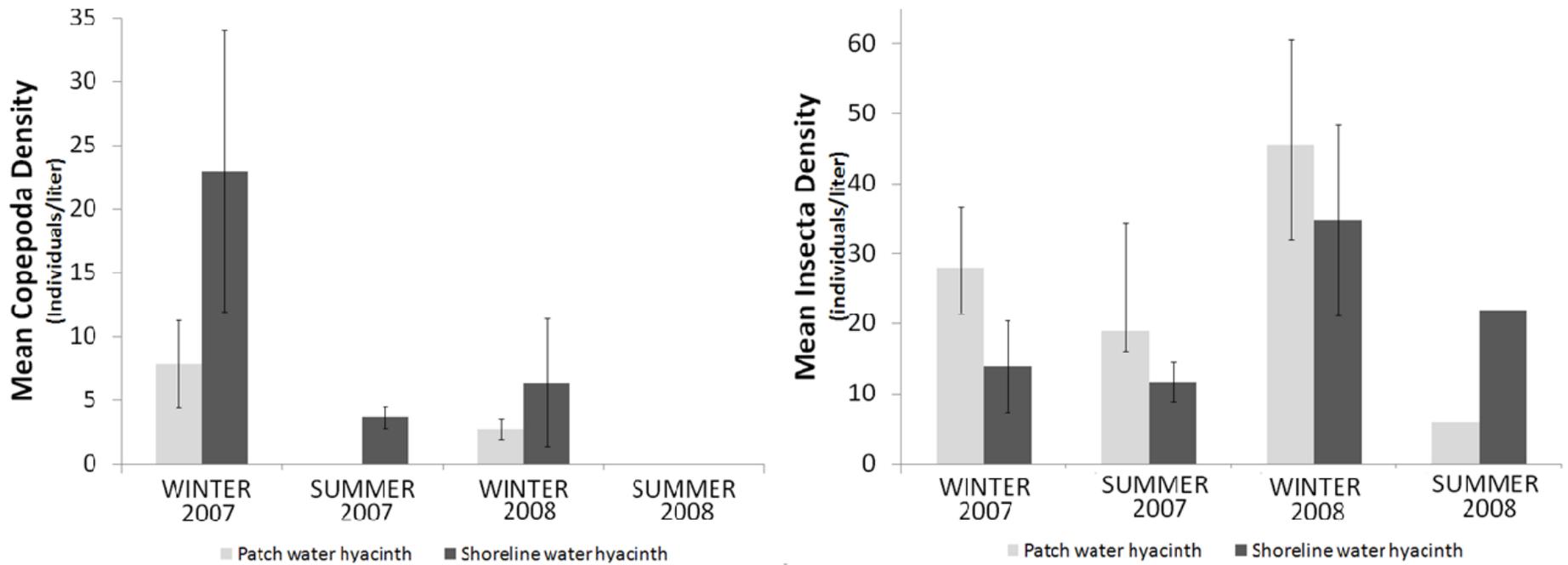


**Fig. 8** Mean density (left) and taxonomic richness (right) of invertebrates within the roots of patch and shoreline water hyacinth at Lake Chapala, Mexico. Bars represent standard error.



**Fig. 9** The relationships between water hyacinth mass and total root invertebrate density.

There were no significant differences in root invertebrate density between patch and shoreline water hyacinth for any of the individual invertebrate groups identified in this study; however there were some notable differences. Copepoda were in higher densities within shoreline water hyacinth throughout the study. In contrast, insects (collectively) were in higher densities within the roots of patch water hyacinth (Fig. 10).



**Fig. 10** Mean density of Copepoda (left) and Insecta (right) in patch and shoreline water hyacinth collected from Lake Chapala, Mexico. Bars represent standard error.

## Discussion

Invertebrate density within the water column

### *Differences among habitat types*

As expected, we found more invertebrates at the edge and within water hyacinth than in open water during winter 2007; however, this was not the case during any other season. The opposite was found in summer 2007 when invertebrates were more abundant in open water than at the edge or within water hyacinth. There is no clear explanation for such a difference. Water hyacinth cover decreased from 11.4% on average to 4.6%, but there were also abiotic changes attributed to seasonal changes that were not accounted for during this study. No water hyacinth was available for sampling in summer 2008 so we cannot exclude seasonal variability as a potential driver for our invertebrate results. The low density of invertebrates within water hyacinth in summer 2007 may have been caused by the drastic decrease in lake volume and surface area, leaving much of the shallow zone of winter 2007 dry. Water hyacinth was found mostly along the shoreline in summer 2007, so it is possible that the combination of drought and far reaching shallow water negatively affected invertebrates within water hyacinth along the shoreline.

### *Differences at the edge of and within vegetation*

Greater invertebrate density was found at the edge of water hyacinth, when available, than other vegetation types throughout this study. We believe the complexity of water hyacinth roots compared to emergent vegetation and submerged trees was at least partially responsible for supporting a greater density of invertebrates. A similar pattern was detected for samples taken within vegetation, but as water hyacinth density decreased so did the opportunity to sample from within mats. Water hyacinth was only found as “patches” of solitary plants or as clusters of two or three plants along shore in winter and summer 2008. It was nearly impossible to get a full sample without disturbing the benthos when water hyacinth mats along shore were small. Despite sampling difficulty, the results of this study were as expected with greater invertebrate density associated with the more complex vegetation structure of water hyacinth.

### Taxonomic richness within the water column

### *Differences among habitat types*

As expected, we found more taxonomic groups in samples taken at the edge of water hyacinth than at the edge of other types of aquatic vegetation, but was not the case for samples taken from within water hyacinth. Taxonomic richness increased throughout the study for all habitat types, except for within-water-hyacinth samples in summer 2007 where mean richness was low and variability high. Richness in open water was greater in seasons with less water hyacinth; however, it was never greater than in water hyacinth, at the edge or within. This may

be because water hyacinth attracted some taxa away from open water, explaining the fact that richness within and at the edge of water hyacinth remained high even in winter 2008 when water hyacinth availability was low. Taxonomic richness was highest at the edge of water hyacinth and during seasons of low to moderate water hyacinth cover. This may be explained by the intermediate cover hypothesis (ICH) that was developed to explain fish density and diversity (Miranda & Hodges, 2000, Grenouillet et al., 2002) but also might be applicable to invertebrates. The ICH suggests that fish density increases as a function of increased prey density and the provision of refuge from predators, both attributed to increased vegetation (Savino & Stein, 1982, Savino et al., 1992). However, fish density is then limited by an increase in intra- and interspecific competition and decreased dissolved oxygen that results when vegetation cover gets too high (Crowder et al., 1982). The same idea could be adopted for invertebrates since increases in substrate availability increase growth of epiphytic algae, bacteria, and invertebrates, provide refuge from fish predators, and at high densities, can cause low dissolved oxygen conditions by shading out the water column. In the Miranda and Hodges study (2000), macrophytes covered up to 91% of the study area. Water hyacinth cover was measured at the site-level in this Lake Chapala study, therefore the relationships between cover and fish productivity are not directly transferrable.

#### *Differences at the edge of vegetation*

The results from the vegetation analysis also confirmed our expectation of greater diversity in water hyacinth than in emergent vegetation or submerged trees. Invertebrate assemblages at the edge of shoreline water hyacinth were most diverse in winter and summer

2007, significantly more than emergent vegetation in both seasons and more than patch water hyacinth in winter 2007. Taxonomic richness was highest at the edge of patch and shoreline water hyacinth for all seasons when water hyacinth was present, thus supporting the claim that water hyacinth increases invertebrate diversity.

### *Differences within vegetation*

We did not detect a clear pattern for samples taken from within vegetation. The fact that samples were only significantly richer in shoreline water hyacinth than emergent vegetation during winter 2007 suggests that complexity as a function of water hyacinth density and spatial configuration of the mats may play a role in determining taxonomic richness. This hypothesis is also supported by the pattern detected for patch water hyacinth and emergent vegetation. Patches of water hyacinth were larger and denser in winter 2007 than during any other season; thus, there were obvious structural differences between emergent vegetation stands and floating mats of water hyacinth during winter 2007. As water hyacinth cover decreased, the size of the patches decreased, and the spaces between plants increased. There was little difference in invertebrate richness between emergent vegetation and patch water hyacinth in summer 2007 when mean site-level water hyacinth cover was less than 5% and most water hyacinth was found along the shoreline and in much smaller patches. The trend continued and in winter 2008, when mean cover was less than 3%, samples from emergent vegetation were more taxonomically rich than those taken from patch water hyacinth, and were roughly as rich as samples from shoreline water hyacinth. We found little difference in taxonomic richness between emergent vegetation and submerged trees in summer 2008; however, in the first two seasons, diversity within submerged

trees was higher than emergent vegetation. We attribute the initial differences to the greater surface area for epiphytic algae and invertebrates associated with submerged trees than with emergent vegetation. Many submerged trees retained partial foliage that increased the complexity of the vegetation and likely provided more refuge opportunities than the simple structure of emergent like cattail. It is also possible that when water hyacinth was not available, invertebrates colonized submerged trees and emergent vegetation equally, perhaps suggesting a habitat preference for water hyacinth when available.

#### Invertebrate Assemblages within the water column

Water hyacinth's influence on invertebrates appears to be density dependent based on the results of this study. The most obvious and statistically significant differences in invertebrate assemblages were detected during winter 2007 when water hyacinth cover was greatest. During seasons of extensive water hyacinth cover, the physical difference among habitat types was well defined. As water hyacinth cover decreased, the physical difference among habitats became less clear and we noticed a decrease in the magnitude of differences in invertebrate assemblages.

Water hyacinth clustered densely along shorelines and was found in large floating mats that were surrounded by open water during winter 2007; however, it was common for large floating mats to merge to form larger floating mats, especially as these mats approached shore. Less water hyacinth was present and floating mats were smaller in summer 2007. Edge length and the area within a mat decreased as mat size decreased. A decrease in edge and within habitat meant a decrease in available refuge area where invertebrates were protected from outside conditions and

predation. It also meant increased interaction between water hyacinth and open water. We attribute the loss of distinction among habitat types to the combination of these three factors.

### *Taxa-specific responses*

As expected based on previous studies, invertebrate groups differed in abundance among habitat and vegetation types; however, copepods were the dominant invertebrate group found in all habitat types throughout this study. These results agree with Trotter (1988) who found calanoid copepods to be in highest abundance in among study sites in Lake Chapala between September and December 1983; larger invertebrates were not included in the Trotter (1988) study. Non-dominant invertebrate groups, including Diptera larvae, Coleoptera, annelids, amphipods, and gastropods (Fig. 10, top left), were most dense at the edge and within water hyacinth during summer 2007. We expected higher densities of these groups to be associated with vegetation and specifically with water hyacinth (Pennak, 1953, Thorp & Covich, 2001) during summer months where spring-emerging taxa (e.g. Coleoptera and Diptera) are prevalent. Many of the taxa that made up the “other” category are common to littoral vegetated zones (Pennak, 1953, Thorp & Covich, 2001). Water hyacinth was primarily found along shorelines in summer 2007; therefore, a larger portion of the samples from the edge and within water hyacinth was taken from shoreline water hyacinth. Non-dominant invertebrate groups represented a smaller portion in winter 2008, but this was not smaller than winter 2007, suggesting the potential influence of seasonality.

The patterns of the 4 dominant invertebrate groups suggest that water hyacinth was not negatively affecting these invertebrates. Three of 4 dominant groups were more abundant during

seasons with at least some water hyacinth present. For example, cladoceran density was highest during seasons with low to moderate water hyacinth cover and lowest during summer 2008. Cladocerans are generally more abundant in and around shoreline vegetation and some are tolerant of low dissolved oxygen concentrations, therefore we did not expect them to be limited by dense water hyacinth mats. The proportion of copepods in the open water was higher in summer 2008, but the total density was not. Water hyacinth may have provided refuge for cladocerans, Eubranchiopoda, and copepods allowing these groups to increase in densities in open water. Rotifers did not have the same pattern; density was greatest in summer 2008. In general, there were no differences in invertebrate density between patch and shoreline water hyacinth except for annelids and gastropods. This could be expected for taxonomic groups like annelids and gastropods, which are strongly associated with vegetation and shallow water (Pennak, 1953, Peckarsky et al., 1990, Thorp & Covich, 2001). It is likely the depth of the water, predation pressure, and other abiotic conditions associated with shallow water, as opposed to the structure of the vegetation alone, drove the significant differences detected in this study.

#### Root invertebrates

As expected, we did not find significant differences in root invertebrate density or taxonomic richness between patch and shoreline water hyacinth. This may be due to the mobility of individual plants and mats within the ecosystem or that structure, rather than the location of the plants, drove invertebrate density and diversity associated with water hyacinth. Invertebrate density was higher in study seasons with low water hyacinth cover. We think this may be

attributed to a water hyacinth density effect discussed earlier. Fewer plants were available and individual plants were isolated from each other in winter and summer 2008 when water hyacinth cover was low, yet root invertebrate density was higher. This suggests that the invertebrate density on an individual plant may be inversely related to the density or percent cover of the water hyacinth mat rather than the actual weight or size of the plant; however, without a better standardized measure of plant size (e.g. root surface area), we cannot be sure. If density or water hyacinth cover was inversely correlated with invertebrate density, optimal management might reduce the density of water hyacinth mats by thinning or selectively harvesting plants, but maintain a low density cover of water hyacinth to provide refuge and substrate for invertebrate colonization.

The higher density of insects and insect larvae on roots of patch water hyacinth than on shoreline plants was contrary to our initial expectation. We expected larvae to be limited to shallow water areas, but perhaps because plants are so mobile this was not the case. Also, it is possible that predation pressure on insects was higher in shoreline areas, but this remains speculative because fish densities associated with water hyacinth are not explicitly known in Lake Chapala. This finding may be important in terms of human health issues associated with insect-borne diseases. First, insect densities were higher within the roots of patches of water hyacinth plants; these patch plants were found within 150 meters of shore, but could float farther from shore depending on wind patterns. Second, insect densities in patch and shoreline plant roots were higher in winter and summer 2008 when water hyacinth cover was low. This suggests that insect abundance, and therefore the threat of transmitting insect-borne diseases, is not positively correlated to water hyacinth cover or density, a common concern often expressed with dense water hyacinth cover.

## Invertebrate-fish relationship

Many of the invertebrate groups sampled in this study represent large dietary components for Lake Chapala's fish, according to Guzman-Arroyo's study (1995). We identified fishes that might be affected by the presence of water hyacinth and how the differences in invertebrate density and composition could increase or decrease prey availability based on the results from our study and dietary preferences of Lake Chapala fish (Guzman-Arroyo, 1995). The common carp (*Cyprinus carpio carpio*), bagre (*Ictalurus dugesi* and *I. ochoterenai*), charal (*Chirostoma spp.*), pescado blanco (*Chirostoma arge*, *C. chapalae*, *C. consocium*, *C. jordani*, and *C. labarcae*), and tilapia (*Oreochromis aureus*) are the fishes most directly affected by changes in invertebrate assemblages. *I. ochoterenai* and *C. chapalae* are endemic to the Lerma-Chapala basin (Froese & Pauly, 2000). The normal diet of the common carp, one of the most abundant fishes in the lake, is generally comprised of fish (26%), aquatic vegetation (22%), gastropods (12%), insect larvae (10%), cladocerans (8%), and copepods (6%). Bagre rely more heavily on insect larvae (21%), fish (12%), crustaceans (35%), and plant matter (12%). The charal is a much smaller fish whose diet consists of arthropods (17%), insects (20%), crustaceans (29%), plant matter (12%), and to a much smaller degree, rotifers (1%) and other invertebrates (3%). Pescado blanco, like the charales, are classified as carnivore; fish alone represent 25% of its diet. Ostracods (9%), insects (8%), copepods (8%), cladocerans (6%), rotifers (2%), crustaceans (14%), and plant matter (12%) comprise the rest of its diet. Tilapia, a non-native fish introduced to bolster fishery production, derives 40% of its diet from phytoplankton and another 33% from plant matter. Copepods and rotifers only make up 3% and 8%, respectively, of this economically important fish (Guzman-Arroyo, 1995).

The differences in invertebrate density and composition that we detected suggest a potential indirect impact on fishes of Lake Chapala. The common carp would likely be the fish species most sensitive to changes in invertebrate assemblages caused by the presence of water hyacinth in Lake Chapala. Gastropods represent more than a tenth of the common carp diet and was only found associated with water hyacinth, mostly along the edge of water hyacinth (Fig. 7, top left). Furthermore, water hyacinth housed more copepods than open water but fewer cladocerans when water hyacinth cover was highest in winter 2007 (Fig. 6, top). Cladocerans represented a slightly greater dietary component for the common carp than copepods, but a decrease could have a potentially negative effect on the fish if it is unable to increase consumption of the more abundant copepods. Overall we might expect the carp's diet to include a greater proportion of gastropods and copepods when water hyacinth is present. However, it should be noted that common carp generally feed on or near lake bottoms; therefore, we would expect water hyacinth's influence to be greatest in shallow waters where the roots are closer to the bottom.

Pescado blanco may also be affected by changes in invertebrate assemblages, despite nearly a quarter of its diet typically being the consumption of other fish. Cladocerans and copepods collectively account for almost 15 % of the pescado blanco diet. Changes in cladoceran and copepod density could potentially affect this species, but they are unlikely to make a major difference because both groups were present with and without water hyacinth. Ostracod density, typically 9% of the pescado blanco diet, differed little in samples taken from the edge of water hyacinth and open water (Fig. 7, top right), but the densities we observed were highly variable suggesting water hyacinth presence alone was not the only driving force for observed densities.

We conclude that water hyacinth's effect on insect populations may have the greatest impact on fish of Lake Chapala. Aside from tilapia, all of the fish species mentioned above rely on insects and insect larvae for 8% to more than 20% of their total consumption. We found a strong relationship between water hyacinth and insects when we combined the densities of Diptera, Coleoptera, and Hemiptera into a single insect group (Fig. 7, bottom). Very few insects or insect larvae were found in open water. This suggests that water hyacinth could greatly increase this food source important to most species in Lake Chapala. While emergent vegetation and submerged trees may also provide such benefits to the fish, the submerged trees will eventually decompose and emergent vegetation is not very abundant around the lake.

## Conclusions

From this study we conclude that 1) the presence of water hyacinth in Lake Chapala affected invertebrate distribution and habitat use; 2) the presence of water hyacinth generally increased density of dominant invertebrates, with the exception of rotifers; 3) water hyacinth may have affected invertebrates in open water as well as those directly associated with the plant; 4) the density and size of water hyacinth mats appear to have played an important role in determining invertebrate density, diversity, and assemblage composition, but additional sampling during times of high water hyacinth cover is needed to validate this claim; and 5) water hyacinth did not appear to have direct negative impacts on invertebrates or fishes of Lake Chapala. Prior to the first season of sampling, herbicides were applied to water hyacinth mats along the lake shoreline of Jalisco state. As the availability of water hyacinth in Lake Chapala decreased from a seasonal mean of 11.4% site cover to less than 0.5% over, so did the opportunity to detect

differences in invertebrate assemblages. In general, the differences detected in density and species richness were during winter and summer 2007 when water hyacinth density was still relatively high. During these seasons the physical differences among habitat types were clearly defined. As the percent cover decreased, mat size decreased and patches were interspersed with greater open water areas. The fragmentation and decreased size of mats likely contributed to our results, but these factors were not explicitly measured. Furthermore, water hyacinth mats were extremely mobile. Patches of water hyacinth often joined shoreline mats, making it difficult to decipher among habitat types. In this study we assumed an immediate invertebrate response to the presence of water hyacinth but expect the persistence of water hyacinth at a given site may have contributed to invertebrate density and assemblage composition. We used seasonal water hyacinth means to try to account for the effect of water hyacinth persistence. Future studies should try to explicitly incorporate site-level water hyacinth persistence as a potential factor influencing invertebrate assemblages by sampling each site more than once a season.

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## Chapter 5

### Effects of water hyacinth on dissolved oxygen concentrations and water transparency at Lake Chapala, Mexico

**Keywords** Water hyacinth, invasive plants, dissolved oxygen, water transparency, Secchi depth

#### Introduction

As a free-floating macrophyte, water hyacinth has a strong competitive advantage over phytoplankton and submersed vegetation because it intercepts light at the surface and has a strong capacity for nutrient uptake (Gopal, 1987, Aoi & Hayashi, 1996, Zimmels et al., 2007). Floating mats of water hyacinth create a canopy that shades the water column, preventing phytoplankton and submersed vegetation from obtaining light for photosynthesis (Rommens *et al.*, 2003). Unlike other aquatic macrophytes and phytoplankton, water hyacinth does not release oxygen into the water column (Gopal, 1987). In addition to reduced dissolved oxygen production, biological respiration within water hyacinth mats is higher than in open water as a result higher invertebrate and fish density (Perna & Burrows, 2005, Bicudo et al., 2007). Prior studies suggest that water hyacinth can drastically decrease dissolved oxygen concentrations under mats. Based on these studies, I expect higher dissolved oxygen concentrations in open water than at the edge or within water hyacinth mats (Masifwa et al., 2001, Perna & Burrows, 2005). Furthermore, I expect an inverse relationship between percent water hyacinth cover and

dissolved oxygen concentrations in open water (McVea & Boyd, 1975, Miranda & Hodges, 2000) and dissolved oxygen concentrations to be higher during winter seasons when water temperatures are cooler.

Water transparency is an attractive quality in water bodies that are used primarily for recreation or drinking water. Water clarity is also an indicator of potential primary productivity, with lower productivity associated with more transparent water. Although macrophytes are generally shown to reduce suspended particles (Carpenter & Lodge, 1986, Madsen et al., 1996) and water hyacinth is thought to increase water transparency by reducing phytoplankton productivity (Rommens *et al.*, 2003), water hyacinth may actually increase suspended turbidity by entrapping sediment, existing phytoplankton, and detritus (Rommens et al., 2003, Bicudo et al., 2007). There are few studies that explicitly report the effect of water hyacinth mats on water transparency. In this study, I tested for differences in dissolved oxygen concentrations and water transparency in open water areas with respect to site-level percent water hyacinth cover and for differences in among habitat types: open water, the edge of water hyacinth mats, and within water hyacinth mats. I also examined dissolved oxygen patterns to determine whether water hyacinth cover was responsible for concentrations below critical thresholds for aquatic organisms. Concentrations lower than  $4.8 \text{ mg L}^{-1}$  are considered detrimental to fish growth and concentrations lower than  $2.3 \text{ mg L}^{-1}$  threaten juvenile and adult survival according to the US EPA water quality criteria for dissolved oxygen criteria (1986).

## Methods

### *Dissolved oxygen*

I measured dissolved oxygen at the ten randomly-selected sampling sites during June 2007, February 2008, and June 2008 (Table 2) to 1) determine the effects of water hyacinth cover on open water dissolved oxygen concentrations (broad-scale), and 2) determine whether dissolved oxygen concentrations varied among habitat types: open water, the edge of water hyacinth, and within water hyacinth. I measured dissolved oxygen at various sampling points within each habitat type at sunrise, midday, and sunset at each site and calculated mean dissolved oxygen concentration (percent saturation) for each habitat type and time period. I conducted an analysis of variance (ANOVA) to test for seasonal differences in dissolved oxygen in open water at each site during each sampling period. The expectation based on prior studies was that open-water dissolved oxygen concentrations would be lower at sites with greater water hyacinth cover (Miranda & Hodges, 2000, Perna & Burrows, 2005). I tested for differences in dissolved oxygen concentrations among habitat types for each season also using an ANOVA. I also calculated seasonal mean water hyacinth cover for each site to compare seasonal cover to dissolved oxygen concentrations (Chapter 4, Fig. 1).

**Table 1** Ten dissolved oxygen and water transparency study sites around Lake Chapala, Mexico.

Site Name	Acronym	Shoreline location	Coordinates (longitude, latitude)	
Ajijic	AJI	NW	20.2959	-103.2620
Jocotepec	JOC	W	20.2837	-103.4138
Mezcala	MEZ	NC	20.3343	-103.0288
San Cristobal Zapótitlan	SCZ	SW	20.2274	-103.3745
San Juan Cósala	SJC	NW	20.2849	-103.3425
San Luis Sóyatlan	SLS	SW	20.1985	-103.3032
San Nicolas	SN	SC	20.1920	-103.2540
San Pedro Tésistan	SPT	SW	20.2311	-103.4121
Palo Alto	PAL	SE	20.1666	-102.9270
Tecómatlan	TEC	NC	20.3234	-103.0995

### *Water transparency*

I measured water transparency using a Secchi disk during summer 2007, winter 2008, and summer 2008 at the same ten sites around Lake Chapala. I measured Secchi depth at midday at various randomized locations within each site on one day per season. At least three measurements were taken at each site within open water, at the edge of water hyacinth, and within water hyacinth mats (when available).

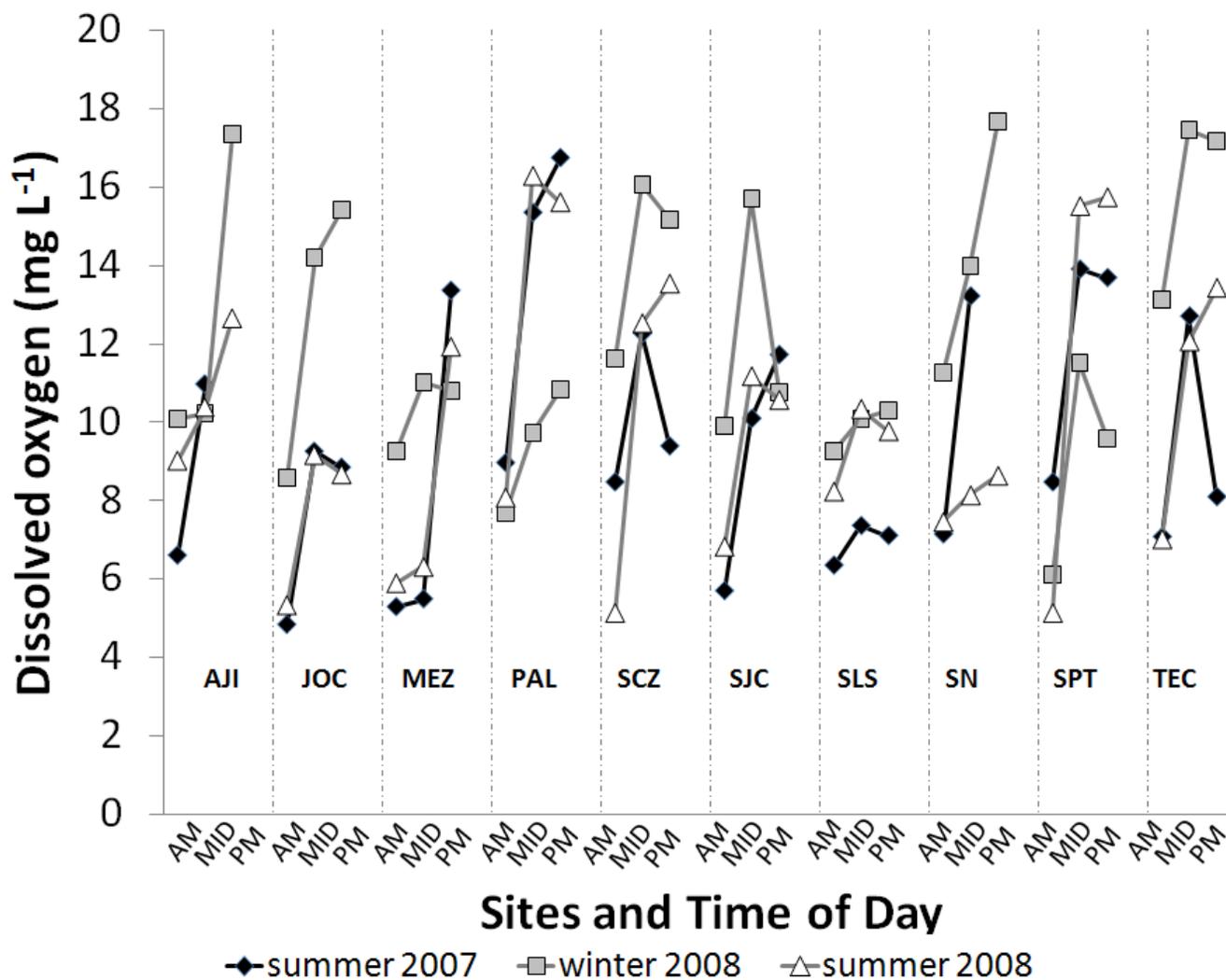
## Results

### *Open water dissolved oxygen*

As expected, daily dissolved oxygen concentrations in open water were generally higher in winter 2008 than the other two summers, except at Palo Alto (PAL). Dissolved oxygen concentrations at sunrise were significantly lower in summer 2007 than summer 2008 at 3 of ten sites (AJI, SJC, and SLS). Of these 3 sites, SJC and SLS had less than 1% water hyacinth cover during both summers. Dissolved oxygen concentrations at sunset were also significantly lower in summer 2007 than summer 2008 at 3 sites (SCZ, SLS, and TEC), but SCZ and SLS both had less than 1% water hyacinth cover during both seasons (Fig. 1).

### *Dissolved oxygen among habitat types*

The dissolved oxygen analysis among habitat types was limited to the summer 2007 and winter 2008 sample seasons due to low water hyacinth availability in summer 2008. I found significantly higher dissolved oxygen concentrations in open water than at the edge of or within water hyacinth at sunset during both seasons. Sunrise dissolved oxygen concentrations were significantly higher in open water than within water hyacinth or at the edge of water hyacinth during summer 2007 (Table 4). Dissolved oxygen was highest at midday for all habitat types and seasons except in open water during winter 2008, but the difference was not significant (Fig. 5). Dissolved oxygen concentrations were lower at sunset than midday at the edge of and within water hyacinth mats during both seasons.



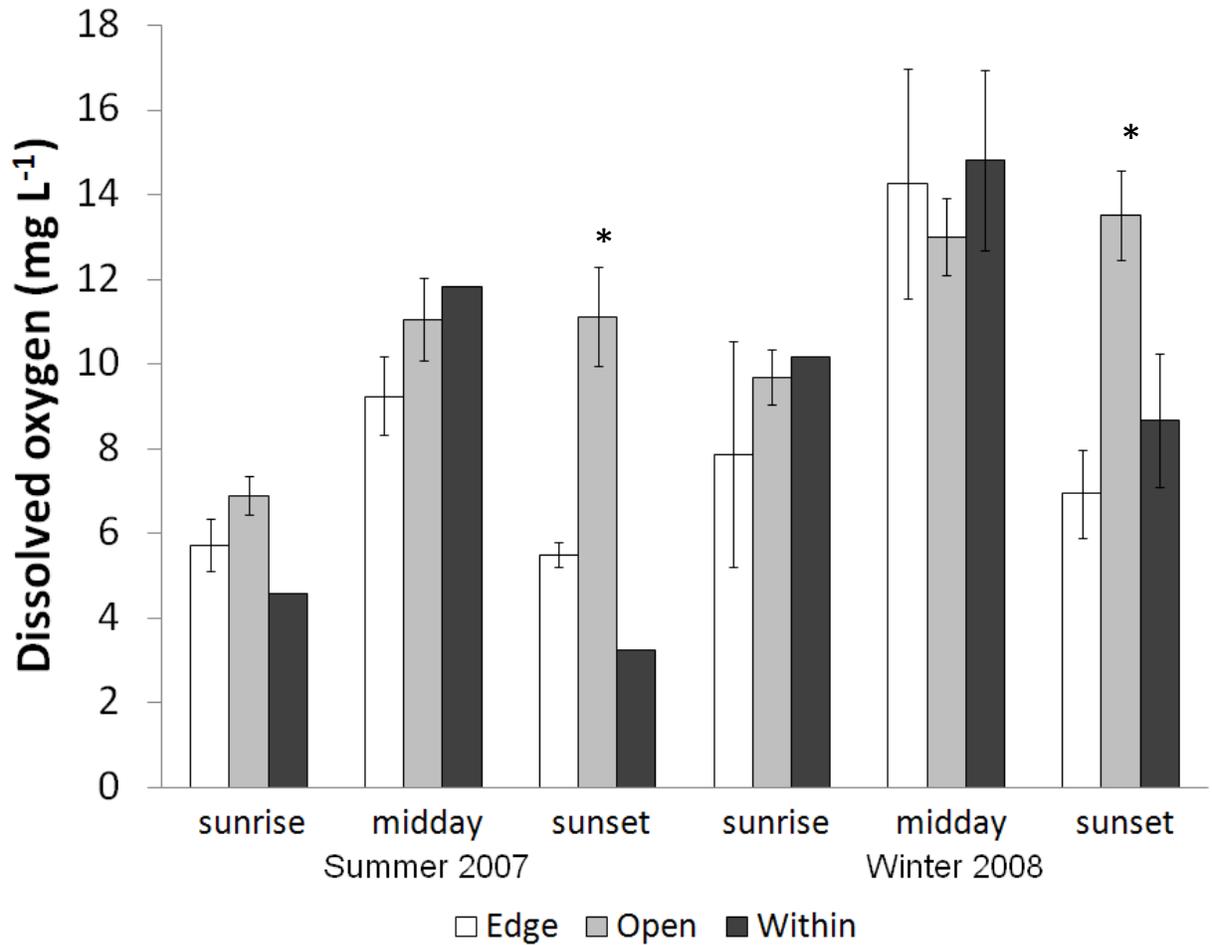
**Fig. 1** Daily dissolved oxygen patterns in open water at ten sites around Lake Chapala, Mexico during summer 2007, winter 2008, and summer 2008. AM: sunrise, MID: midday, and PM: sunset.

**Table 2** Statistical comparison (P-values) of dissolved oxygen among seasons at ten sites around Lake Chapala, Mexico. "S 2007" = summer 2007, "W 2008" = winter 2008, and "S 2008" = summer 2008. "NS" represents an insignificant difference ( $\alpha \geq 0.05$ ) and "NA" represents no data available for comparison.

Sites	Sunrise		Midday				Sunset		
	S 2007	W 2008	S 2007	S 2007	W 2008	S 2007	S 2007	W 2008	S 2007
	S 2008	S 2008	W 2008	S 2008	S 2008	W 2008	S 2008	S 2008	W 2008
AJI	0.0013	NS	0.0006	NS	0.0293	0.0053	<.0001	NA	NA
JOC	NS	0.0476	0.0196	NS	0.0045	0.0015	NS	<.0001	<.0001
MEZ	NS	0.0003	<.0001	0.013	<.0001	<.0001	0.0375	0.0484	0.0007
PAL	0.0014	0.0008	<.0001	NS	<.0001	<.0001	NS	<.0001	<.0001
SCZ	<.0001	<.0001	<.0001	NS	0.0209	0.0029	0.0001	NS	<.0001
SJC	0.0006	<.0001	<.0001	0.0061	0.0006	<.0001	NS	NS	0.0211
SLS	<.0001	NS	<.0001	<.0001	0.0376	0.0046	<.0001	NS	<.0001
SN	NS	<.0001	<.0001	0.0189	NS	NS	NA	<.0001	NA
SPT	<.0001	NS	<.0001	NS	0.0008	0.008	0.0026	<.0001	<.0001
TEC	NS	<.0001	<.0001	NS	0.0001	0.002	<.0001	0.0231	<.0001

**Table 3** Statistical comparison (P-values) of dissolved oxygen concentrations among open water, edge of water hyacinth, and within water hyacinth for summer 2007 and winter 2008 on Lake Chapala, Mexico. NS represents a non-significant difference.

Time of Day	Summer 2007			Winter 2008		
	Edge Open	Edge Open	Within Open	Edge Open	Edge Open	Within Open
Sunrise	NS	0.0422	0.0002	NS	NS	NS
Midday	NS	NS	NS	NS	NS	NS
Sunset	<.0001	NS	<.0001	0.0007	NS	0.0152



**Fig. 2** Mean dissolved oxygen concentrations among habitat types at sunrise, midday, and sunset during summer 2007 and winter 2008 on Lake Chapala, Mexico. Bars represent standard error. \* denotes significant difference.

#### *Critical dissolved oxygen concentrations*

Mean dissolved oxygen concentrations were below critical levels for fish growth within water hyacinth at sunset in summer 2007. During this season, 11 sunrise samples from 5 sites were below 4.8 mg L<sup>-1</sup>, and dissolved oxygen concentrations were less than 2.3 mg L<sup>-1</sup> on two of these occasions. Of these five sites, only AJI and TEC had more than 10% water hyacinth cover on average during summer 2007. Dissolved oxygen concentrations fell below the 4.8 mg

L<sup>-1</sup> threshold on 5 occasions at sunset in summer 2007, all at Ajijic (AJI) where water hyacinth covered 17% of the site. Dissolved oxygen concentrations fell below 4.8 mg L<sup>-1</sup> only on 3 occasions in winter 2008, 2 of which were at sunrise at AJI and JOC. On average, water hyacinth covered almost 5% of JOC and less than 1% at AJI during winter 2008. In summer 2008, JOC was the only site where dissolved oxygen concentrations fell below the 4.8 mg L<sup>-1</sup> threshold, but there was no water hyacinth cover at JOC during this season.

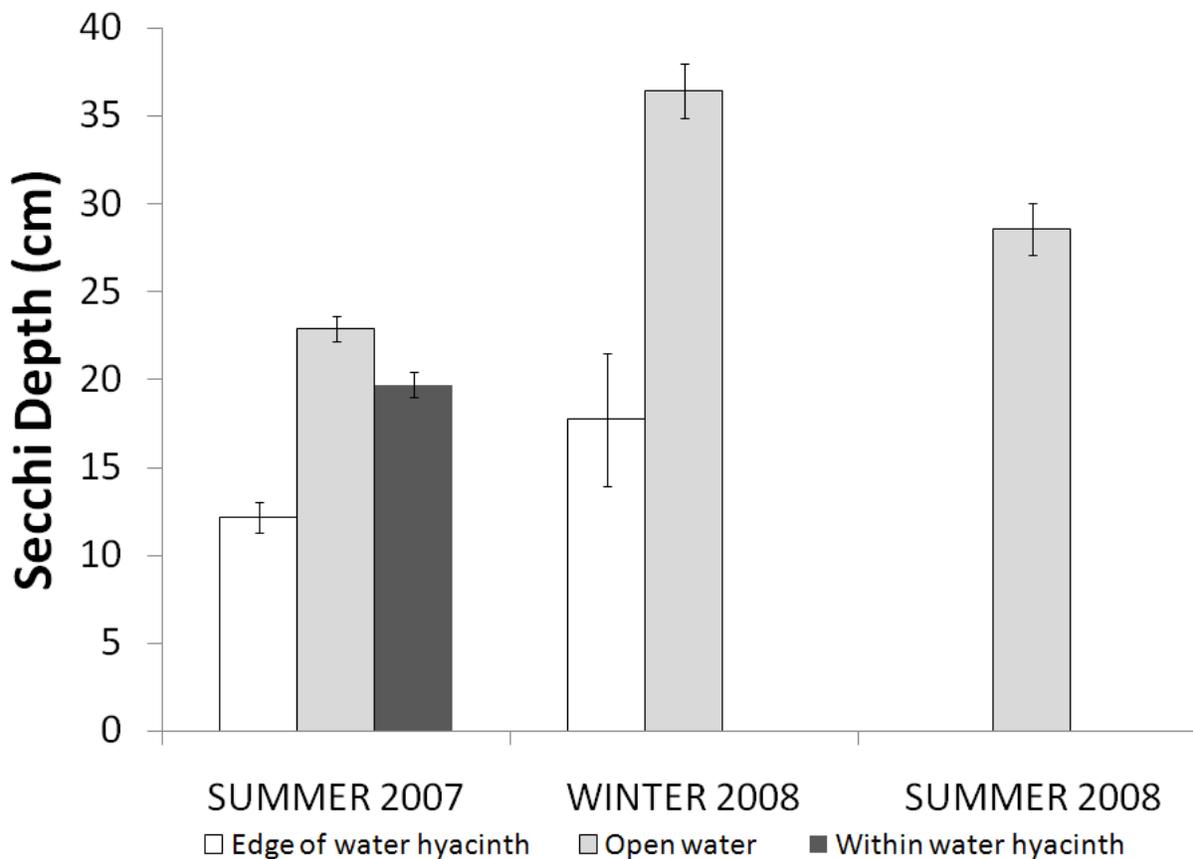
*Water transparency*

My examination of water transparency differences among habitat types was limited to summer 2007 during which all three habitat types were available to be sampled. I aggregated data since water hyacinth was limited to a few sites. I only measured Secchi depth at the edge of water hyacinth and in open water in winter 2008 and only in open water in summer 2008 due to the lack of water hyacinth (Fig. 6). I found a significant difference in water transparency between open water and the edge of water hyacinth during summer 2007 and winter 2008, but I found no difference in transparency between the edge and within water hyacinth or between open water and within water hyacinth (Table 5).

**Table 4** Statistical comparison (P-values) of water transparency among habitat types at ten sites around Lake Chapala, Mexico. NS represents non-significant differences ( $\alpha \geq 0.05$ ).

Seasons	Edge Open	Edge Within	Within Open
Summer 2007	0.0018	NS	NS
Winter 2008	0.0079	no within samples	
Summer 2008	only open water samples		

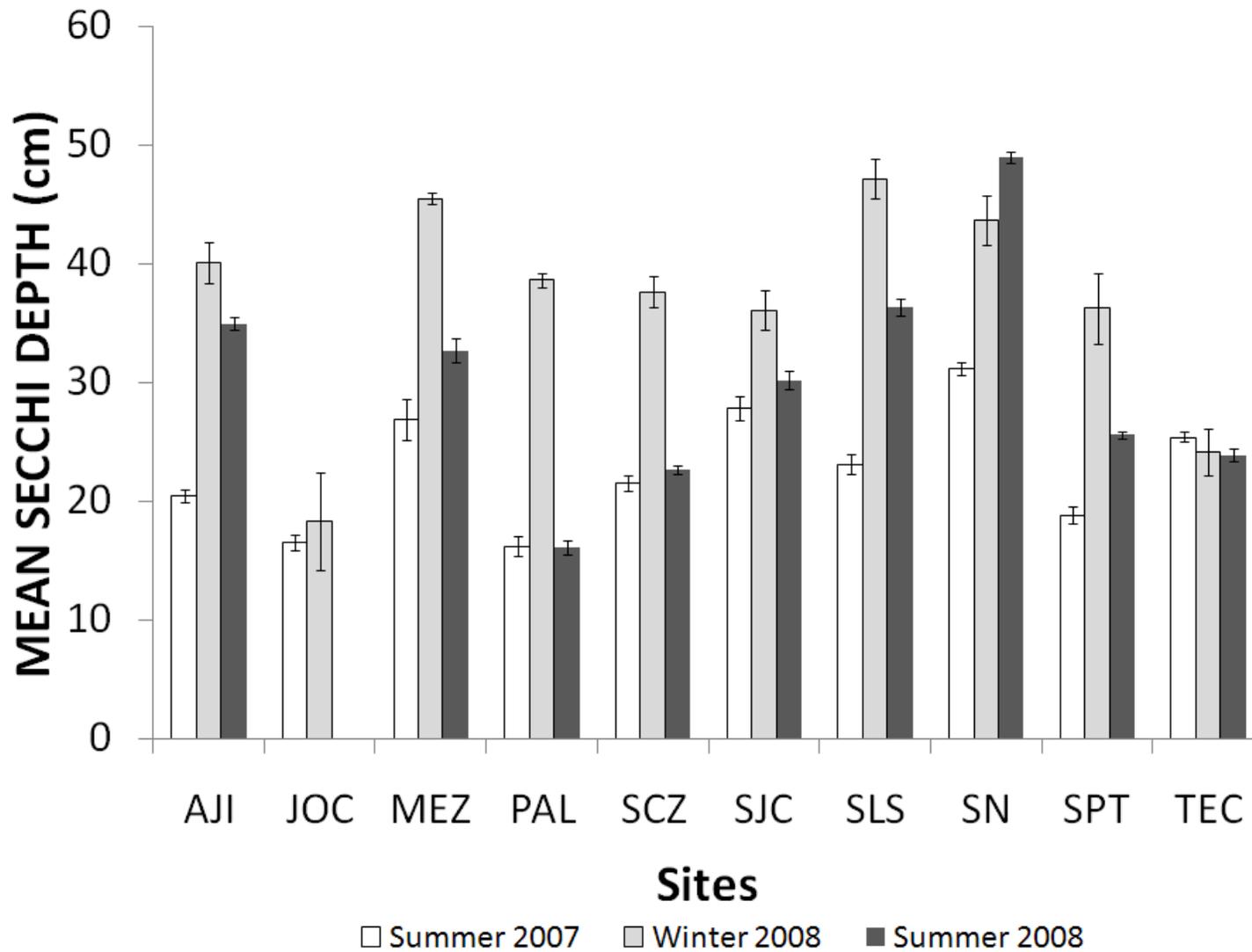
I found that open water areas were significantly more transparent in winter 2008 than both summers (2007 and 2008) at eight of ten sites (Table 6). Similarly, water was more transparent in summer 2008 than summer 2007 at five of nine sites (data for JOC was not available). Some of the sites where water was significantly more transparent in summer 2008 than summer 2007 are those at which little water hyacinth ever existed. SN, SPT, and SLS did not contain more than 1% water hyacinth in either season. Secchi depth at MEZ and AJI was significantly less in summer 2007 (Fig. 7) when mean water hyacinth covered 5% and 17% more site area, respectively.



**Fig. 3** Mean Secchi depth for open water, water hyacinth's edge, and within water hyacinth at ten sites around Lake Chapala, Mexico. Bars represent standard error.

**Table 5** Statistical comparison (P-values) of Secchi depth in open water at ten sites around Lake Chapala, Mexico. NS represents non-significant differences ( $\alpha \geq 0.05$ ).

Sites	Summer 2007 - Summer 2008	Winter 2008 - Summer 2008	Summer 2007 - Winter 2008
AJI	<.0001	0.0197	<.0001
JOC	NS	NS	NS
MEZ	0.0332	0.0009	<.0001
SJC	ns	0.0044	0.0003
SLS	<.0001	0.0002	<.0001
SCZ	NS	<.0001	<.0001
SPT	0.0043	0.0003	<.0001
SN	<.0001	0.0062	<.0001
TEC	NS	NS	NS
PAL	NS	<.0001	<.0001



**Fig. 4** Mean Secchi depth at ten sites around Lake Chapala during summer 2007, winter 2008, and summer 2008. Bars represent standard error.

## **Discussion**

### *Dissolved oxygen*

As expected, mean dissolved oxygen concentrations in open water were higher at midday and sunset than at sunrise. This was not the case at the edge of or within water hyacinth. Dissolved oxygen concentrations initially increased between sunrise and midday within these habitats, but subsequently fell after midday. This suggests either that 1) oxygen production via phytoplankton and submersed vegetation photosynthesis was constrained after midday, 2) biological respiration at the edge of and within water hyacinth exceeded oxygen production, or 3) a combination of the first two. Furthermore, open water dissolved oxygen concentrations only exceeded those at the edge of and within water hyacinth in summer 2007 when average seasonal water hyacinth cover was 4.6% at these sites, the highest observed during the dissolved oxygen study. This suggests that the density of water hyacinth mats may have contributed to the observed differences among habitat types.

Low dissolved oxygen concentrations can be detrimental and potentially fatal to fish and aquatic invertebrates. I found few instances in which low dissolved oxygen was clearly associated with water hyacinth. Of 22 occasions when dissolved oxygen concentrations were less than 4.8 mg L<sup>-1</sup>, only 9 were at sites with more than 10% water hyacinth cover (AJI and TEC). These sites are also located on the northern shore of the lake where human density is highest. This suggests that water hyacinth was not the only factor causing low dissolved oxygen levels. The open water analysis also did not find substantial evidence linking dissolved oxygen to water hyacinth cover. It would be expected that dissolved oxygen concentrations would be lower in summer 2007 than 2008 based on mean water hyacinth cover at the 10 sites. However, this

was not the case at 9 of 10 sites. These results lead me to conclude that percent water hyacinth cover was not driving dissolved oxygen concentrations in open water at Lake Chapala during this study.

#### *Water transparency*

Water transparency has not been widely studied in conjunction with water hyacinth. Theoretically, macrophytes are expected to increase water transparency by decreasing suspended particles, including phytoplankton, but water hyacinth is capable of trapping detritus and sediment particles, causing the water to be cloudy. Lake Chapala is known as a highly turbid lake with strong seasonal and daily winds currents (Lind & Davalos-Lind, 2001, Lind & Davalos-Lind, 2002). Phytoplankton productivity is naturally limited under these conditions; therefore, it is reasonable to expect that water hyacinth had little effect on phytoplankton productivity and water transparency. Water was more transparent in winter 2008 than summer 2008 at many sites and water hyacinth cover was generally higher in winter 2008 (Chapter 4, Fig. 1). However, there were few differences in site water transparency between summers despite substantial decreases in water hyacinth cover. This suggests that factors other than water hyacinth cover are driving water transparency. In addition to the natural turbid state Lake Chapala is a shallow lake that experiences large seasonal fluctuations in surface area and depth (Lind & Davalos-Lind, 2002). In general, lake levels are lower in summers than winters because the rainy season begins in mid to late June and continues through September. However, lake levels were extremely low in summer 2007 as a result of a regional drought and over-allocation of water resources upstream. By winter and summer 2008 the lake had regained much of its volume and the shoreline water levels were higher, but again summer levels were lower than winter (CEA-Jalisco, 2008). The seasonal pattern in water volume may also be contributing to the increased

transparency during the winter, especially considering the turbidity effect of precipitation upstream during the summers. While this study did not explicitly measure other factors (e.g. precipitation and wind velocity), I suggest that water hyacinth cover was not the primary determinant of water transparency at the site-scale. Furthermore, if the percent cover of water hyacinth on the lake as a whole was a determinant of site-level transparency one could expect to see water clarity patterns that were more uniform among sites than those observed in this study. Therefore, this study concludes that 1) water transparency at the site-level is driven by more than site-level water hyacinth cover (e.g. configuration of mats, precipitation, lake depth, etc.), 2) water transparency may be affected by seasonal climatic differences, and 3) percent water hyacinth cover of the lake is not an appropriate indicator of water hyacinth effects on water transparency.

### *Conclusion*

Overall, my results contradicted expectations and other studies conducted on the effects of water hyacinth on dissolved oxygen and water transparency. This may be attributed to several limnological characteristics (e.g. fetch, turbidity, surface area to depth ratio, etc.) of Lake Chapala that cause greater air-water interaction and mixing within the lake than in other waterbodies where water hyacinth has been studied. Alternatively, it may be that site-level water hyacinth cover was not high enough or that the spatial distribution of water hyacinth mats was not sufficient to cause major changes in dissolved oxygen concentration or water transparency. As water hyacinth cover decreased throughout this study, likely a result of herbicide applications that I first observed in January 2007, the density of mats decreased making the distinction among

habitat types less distinct. Water hyacinth mats were very mobile in Lake Chapala during this study; therefore, the fluidity and consistent movement of mats may have reduced the influence of water hyacinth on water transparency and dissolved oxygen in this system.

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## Chapter 6

An ecosystem overview of the effects of water hyacinth (*Eichhornia crassipes*) on Lake Chapala, Mexico

**Keywords** Invasive species, Water hyacinth, *Eichhornia crassipes*, ecosystem, Freshwater

### Introduction

Invasive species pose an immediate threat to freshwater resources, biodiversity, and society worldwide (Scheffer *et al.*, 1993) as a result of greater connectivity within our modern world (i.e., globalization) (Bright, 1999). Invasive species management primarily focuses on minimizing socioeconomic damages in ways that are least costly. However, the reality is that most non-native species, especially smaller species and those that are difficult to see, are nearly impossible to eradicate once established. In many cases trophic structure, food webs, and energy pathways are changed once the non-native becomes established, sometime permanently (Scheffer *et al.*, 1993). Managers are faced with a difficult choice of how to allocate limited resources among invasive species threats. Managers must prioritize control efforts, especially in aquatic systems where changes can drastically affect human well-being. We must understand the consequences and drivers of invasion in order to decide which species should receive attention and what course of action is most appropriate (Parker *et al.*, 1999). Unfortunately, invasive species management is predominantly reactive and rarely proactive; moreover, management is often initiated in the absence of adequate understanding. Quick responses to invasive species issues that lack the support of strong ecological understanding can lead to the inefficient allocation of time and effort, and in some cases can further complicate the problem.

The systematic investigation of invasive species has to date been ineffective at capturing large-scale effects. Scientists tend to specialize, compartmentalize, and only focus on components of larger problems, while managers are forced to deal with the big picture. This is partially attributed to the difficulty associated with analyzing complex problems but our traditional scientific training is also responsible. By breaking down large problems we isolate components of a functioning system that are otherwise connected; we simplify our studies and analysis at the expense of reality. The overall goal of this 3 year research study was to strengthen our understanding of water hyacinth and how it interacts with important aspects of ecosystem health including water quality, trophic structure, food web structure, ecosystem function, and energy pathways. In this chapter, I synthesize the results of several field studies conducted over the study period and discuss them in an ecosystem context. The objectives, methods, and description of the results are presented in greater specificity in preceding chapters. Here, I focus on the big-picture of water hyacinth in Lake Chapala, reiterate the most relevant results, discuss the interconnectivity among ecological communities, and highlight the implications of this research in the context of water hyacinth worldwide.

### **Water hyacinth around the world**

Water hyacinth (*Eichhornia crassipes*) has been intermittent in Lake Chapala, Mexico, for more than 100 years (CEA-Jalisco, 2005). Water hyacinth is a free-floating aquatic macrophyte native to South America and is recognized as one of the worst aquatic invaders in the world (Center, 1994). Outside of its native range, high densities of water hyacinth can drastically affect the appearance and function of a water body. The plant's distribution and

density is limited by temperature, salinity, and the force of water flow (de Marco *et al.*, 2001; Wilson *et al.*, 2005). It is most problematic in subtropical and tropical inland water bodies with long residence time and high nutrient concentrations (Brendonck *et al.*, 2003; Mangas-Ramirez & Elias-Gutierrez, 2004). Common control efforts include mechanical or manual control (harvesting or in-situ cutting), herbicides (e.g. Diquat, Glyphosate, or 2, 4-D amine), biological control (e.g. *Neochetina eichhorniae* and *N. bruchi*), or some combination of these methods (Seagrave, 1988). No one method is appropriate for all situations; cost, distribution of plants, reoccurrence, and use of the water body should be considered when deciding which course of action is most appropriate. The beneficial (or designated) uses of the waterbody will ultimately influence the management plan, but it is important to understand the consequences of each alternative before deciding (Thayer & Ramey, 1986; Gibbons *et al.*, 1994). There was little research conducted on water hyacinth or its influence on the ecosystem of Lake Chapala prior to this study. Managers decided to control water hyacinth population by mechanical and chemical means in response to the loss of shoreline and navigability caused by large mats along shorelines, in coves, and large patches in deeper water (CEA-Jalisco, 2005). Other commonly perceived effects of water hyacinth include decreased dissolved oxygen concentrations causing fish kills, increased prevalence of insects and insect-borne disease, and decreased aesthetic value (e.g., water transparency). There was little concern about the effects of water hyacinth on biodiversity of Lake Chapala, including waterbirds and fish, at the onset of this study.

In the first chapter, I synthesized prior studies pertaining to water hyacinth dynamics worldwide, both within and beyond its native range. There are several take-home messages from this review. The effects of water hyacinth are directly related to its density or extent of coverage. Its density upon establishment appears to be influenced by environmental conditions including

temperature, salinity, available nutrients, water flow, and predators. Water hyacinth mats can directly affect dissolved oxygen, nutrient concentration, heavy metal and contaminant concentrations, and water transparency (Shine *et al.*, 1998; Rommens *et al.*, 2003; Perna & Burrows, 2005; Tiwari *et al.*, 2007). It can bolster epiphytic algae, zooplankton, and macroinvertebrate populations by creating substrate for colonization, providing prey, and providing refuge (Brendonck *et al.*, 2003), but decrease phytoplankton productivity by removing nutrients and blocking light infiltration (Aoi & Hayashi, 1996; Perna & Burrows, 2005). Mass decomposition of water hyacinth plants, either naturally or management-induced, can drastically decrease dissolved oxygen concentrations beneath mats that can cause fish kills and have a similar effect on oxygen-sensitive aquatic invertebrates (Mangas-Ramirez & Elias-Gutierrez, 2004). The resulting anaerobic conditions can decrease pH causing phosphorous to separate from sediment and reenter the water column, adding to nutrient concentrations and, in many cases, eutrophication (Rodríguez-Gallego *et al.*, 2004). Changing biochemical conditions can have far-reaching effects on the aquatic ecosystem from zooplankton up the trophic ladder to fish, aquatic birds, and humans (Bartodziej & Weymouth, 1995; Brendonck *et al.*, 2003; Toft *et al.*, 2003). Literature suggests that water hyacinth augments invertebrate abundance and in some cases taxonomic richness, especially at the edge of mats where dissolved oxygen concentrations are less likely to reach dangerously low concentrations. Very high densities of water hyacinth can have the opposite effect on invertebrate and fish communities as a result of the unsuitable biochemical conditions beneath extensive mats. In summary, the extent of water hyacinth's impact on an aquatic system is a function of pre-existing ecological structure, function, multi-trophic community dynamics, and water hyacinth cover/density.

## Results from Lake Chapala, Mexico

The second component of this study was an investigation of water hyacinth's effects on waterbirds of Lake Chapala. Specifically, I questioned water hyacinth's effects on waterbird abundance, species diversity, and community composition on two spatial levels: within and among sites. I examined waterbird use of water hyacinth within a site in relation to plant cover (availability) and found that waterbird abundance was positively related to water hyacinth cover during 2 of 7 study seasons. Species diversity was positively and inversely related to cover for 1 season each. Waterbird community composition was only significantly related to water hyacinth cover during the single season with the highest mean cover (winter 2007). I found that all species, with the exception of the Gadwall (*Anas strepera*) during winter 2007, used water hyacinth in proportion to its availability within a given-site, suggesting a benign relationship between the non-native plant and waterbirds. Seasonal waterbird abundance (site-level) was highest during the last two seasons when seasonal water hyacinth cover (site-level) was lowest; however, there was no overwhelming evidence to suggest that waterbirds were being directly affected by water hyacinth. Waterbirds used water hyacinth, thus it appears that the plant did not have direct negative effects on the waterbird community as a whole and the American Coot was the only species (of the four most common species) for which I found an inverse relationship between water hyacinth cover and bird abundance. I did not detect a strong relationship between water hyacinth and waterbirds in Lake Chapala. This suggests a more indirect influence on waterbirds via changes in trophic structure, prey community composition, and energy flows throughout the system. It is also possible that water hyacinth acted on the ecosystem at two spatial levels. Water hyacinth cover provided physical structure for more birds to coexist and changes biochemical conditions within a smaller defined area (e.g. 150 square meters). On a

larger scale, water hyacinth altered trophic structure and community composition, thereby indirectly influencing the waterbird community. This conclusion was supported by increased waterbird abundance with increases in water hyacinth cover during a given season; yet mean waterbird abundance was highest during seasons of low water hyacinth cover. These conflicting results suggest that other factors, that may or may not be attributed to water hyacinth, are impacting waterbirds (e.g., prey availability and the presence of conspecifics).

I sampled aquatic invertebrates in association with various habitat types around Lake Chapala to determine the effects of water hyacinth on potential waterbird prey. According to prior dietary studies, the Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Little Blue Heron (*Egretta caerulea*), Common Moorhen (*Gallinula chloropus*), and American Coot (*Fulica americana*) may be positively affected by increases in prey attributed to water hyacinth. These waterbird species feed on an assortment of crustaceans, aquatic insects (larvae), and mollusks (Willard, 1977; Kushlan, 1978), many of which were in greater abundance at the edge and within water hyacinth than in open water without water hyacinth. Great Blue Herons (*Ardea herodias*) generally feed on fish (Kushlan, 1978) and therefore could be indirectly impacted by water hyacinth if fish abundance increased at the edge of water hyacinth mats. Fish abundance was not explicitly measured in this study and without knowing the specific fish prey of the Great Blue Heron it is difficult to determine how it might be affected.

Larger wading birds, such as the Great Egret, Great Blue Heron, Tri-color Heron, and Snowy Egret, were commonly observed on patches of floating water hyacinth during this study. These patches were surrounded by open water that was deeper than normal foraging grounds. The Great Egret prefers to feed in water approximately 28 cm deep (Custer & Osborn, 1978), the Snowy Egret is generally found feeding in water less than 20 cm deep (Willard, 1977; Kushlan,

1978; Hom, 1983), and the Great Blue Heron hunts for prey from floating objects and in shallow water (Godin, 1977). Water hyacinth is dense and stable enough for even the larger egrets and herons to stand upon; therefore, it is reasonable to suggest that these wading birds used patches as supplemental water access points. Since Snowy Egrets are among the smaller birds in the Ardeidae family and are often outcompeted for space by larger birds, we might expect Snowy Egrets to move to water hyacinth patches where Great Egrets and Great Blue Herons are absent. In this case, water hyacinth would be providing additional habitat that could support greater Snowy Egret abundance. Observations during seasons of moderate to high water hyacinth cover (9-17%) suggest a positive relationship between the abundance of Snowy Egrets on patches of water hyacinth and the abundance of Great Egrets and Great Blue Herons using other habitats within the same site ( $\text{Tau} = 0.215$ ,  $p < 0.0001$ ). The same was true when Snowy Egret abundance was related to the total number of Great Egrets and Great Blue Herons at a given site including patch water hyacinth ( $\text{Tau} = 0.233$ ,  $p < 0.0001$ ). This evidence supports the claim that water hyacinth mats provided additional niche space for subordinate wading bird species, such as the Snowy Egret.

After observing waterbird use of water hyacinth on Lake Chapala during summer 2006, I developed a behavioral study of the American Coot, one of the most abundant waterbird species at Lake Chapala during this study. The goal was to strengthen our understanding of how waterbirds may be using water hyacinth in Lake Chapala. If water hyacinth limited prey availability for American Coots one would expect it to forage in other habitat types and to potentially avoid areas (e.g., study sites) in which water hyacinth cover was high. There was a positive relationship between American Coot use of water hyacinth and the percent cover of water hyacinth within a given site and extensive water hyacinth cover did not affect site choice.

These results suggest that water hyacinth did not deter American Coots. The distinct tie between the proportion of time American Coots used water hyacinth and the proportion of that time spent foraging strongly suggests that the non-native plant provided attractive dietary items.

American Coots were often observed eating water hyacinth leaves. I am unable to say whether this was for plant material or for epiphytic invertebrates, but because the majority of the Coot diet is made up of plant material (Jones 1940), it seems logical that it was at least in part for the former. While animals generally comprise a smaller proportion of the Coot diet, insects, mollusks, arachnids, and crustaceans have been commonly found in stomachs (Jones, 1940; Fitzner *et al.*, 1980; Descrochers & Ankney, 1986). I found all of these invertebrate groups associated with water hyacinth, either from surface water samples taken at the edge of water hyacinth, within water hyacinth mats, or directly from the roots of water hyacinth plants. Many of these invertebrate groups were more abundant at the edge of and within water hyacinth than in open water. Insects and gastropods were virtually non-existent except in association with water hyacinth. In contrast, the abundance of crustaceans, such as branchiopods, copepods, and malacostracans, were variable in water hyacinth. There was little difference in copepod abundance between water hyacinth and open water samples, but brachiopods were more abundant in all samples during seasons of moderate to high water hyacinth cover. In fact, total invertebrate density was greater in open water during seasons with water hyacinth, and was highest in summer 2007 and winter 2008. Overall, it appears that Coots may have benefited from the presence of prey associated with water hyacinth in conjunction with the actual plant material. The results from the invertebrate study support the conclusion that American Coots were not negatively affected by the presence of water hyacinth. I also cautiously suggest that this particular waterbird species may have benefited from water hyacinth; however, I expect the

relationship is non-linear. There is likely a threshold at which water hyacinth cover begins to negatively affect American Coots by decreasing access to prey and prey abundance as biochemical conditions beneath large mats becomes unsuitable.

Although American Coots were observed consuming water hyacinth leaves, it seems unlikely that they would be capable of controlling the water hyacinth population in Lake Chapala, Mexico. Nevertheless, the direct consumption of leaves becomes an issue of ecotoxicology. Lake Chapala is considered highly polluted and is thought to contain elevated concentrations of heavy metals. Moreover, water hyacinth is known to act as a sink for such contaminants. American Coots, and other animals that directly consume water hyacinth plant material, may be at serious risk. Domestic livestock, mainly cattle, may also be at risk because many livestock owners allow their cattle to wade in the lake, drink the water, and eat water hyacinth. This should certainly be investigated to ensure wildlife health, and human health in the case of cattle feeding, around Lake Chapala.

At high density, water hyacinth can out produce and outcompete other aquatic plants and algae. Emergent vegetation and submerged trees persisted at sites around Lake Chapala throughout the study, but they were not present at many sites. Phytoplankton productivity was not directly measured in this study, but mean water transparency in open water was greater in winter and summer 2008 when water hyacinth cover was minimal at most sites. This suggests a negative relationship between water transparency and percent cover on a landscape-scale. However, a closer look revealed that sites with greater clarity in winter 2008 than summer 2007 did not contain extensive water hyacinth mats. Moreover, dissolved oxygen concentrations at the edge and within water hyacinth mats increased throughout the day. The presence changes in water transparency and dissolved oxygen indicate that water hyacinth may have affected

phytoplankton productivity, but it did not eliminate it outright during this study. Furthermore, the results suggest outside factors influencing phytoplankton productivity, dissolved oxygen, and water transparency.

Many people worry that extensive water hyacinth mats increase insect abundance and the prevalence of insect-borne disease. This concern was expressed by state water managers at the onset of this study even though water hyacinth never completely covered the surface of Lake Chapala. This study indicated higher densities of insects and insect larvae during winter 2008 when water hyacinth cover was relatively low. Insect density in patch and shoreline water hyacinth plants during winter 2008 was almost twice as dense as during winter 2007 when water hyacinth cover was abundant. This pattern of insect abundance in the roots of water hyacinth weakens the connection between water hyacinth cover and the threat of increased insect-borne disease.

### **Management Implications**

This study has provided sufficient evidence to support the need for more in-depth analysis of the effects of invasive species prior to major management initiatives. While the holistic approach to understanding water hyacinth's ecological effects on Lake Chapala has broadened our understanding of ecosystem dynamics, it has come at the expense of more in-depth studies or experiments that focus on a single community or species. This study has shown that there have been minimal ecologically negative effects associated with water hyacinth's presence in Lake Chapala during this three year study. However, this does not prove that water hyacinth does not alter the ecosystem. It is possible that my observations reflect the cumulative

impacts of 100 years of intermittent water hyacinth infestations rather than the initial ecological response to water hyacinth's presence. It is difficult to know for sure if water hyacinth is the sole driver of my observed results, but by taking an ecosystem approach I was able to cross-validate my results and look beyond the direct effects commonly studied. Thus, I can conclude that water hyacinth did not have major negative effects on the Lake Chapala ecosystem. It may be that the initial introduction and establishment of water hyacinth in this system caused the system to shift away from historical conditions to resemble what we see today. Such shifts can be permanent (Scheffer *et al.*, 1993) even if water hyacinth were to be eradicated.

Several management recommendations can be made based on the results of this study. First, water hyacinth control in Lake Chapala should reflect its beneficial uses, including ecological health and biodiversity support. Chemical control, while the least-cost method for a single application, is not the most sustainable management option for several reasons: 1) it requires repeated application, 2) plants decompose in the water causing a long list of biochemical changes, including the reduction of dissolved oxygen and release of nutrients, 3) it potentially affects the phytoplankton community, even if only in the short-term, and 4) spraying is limited by precipitation and should only be done in small areas to avoid the aforementioned negative impacts (Seagrave, 1988). Mechanical harvesting appears to be the most sustainable and effective management alternative in the short-term. Mechanical control is highly selective and removal of plants is desirable from a water quality perspective. It is possible to manipulate the configuration of water hyacinth to maintain the benefits of water hyacinth in terms of structure for invertebrates, fish, and birds while minimizing mat clusters along the shoreline that are socioeconomically detrimental. The results from this study, particularly the comparison of invertebrates among open water, water hyacinth's edge, and within water hyacinth, suggest that

an increase in water hyacinth edge while minimizing the area beneath a mat (termed *within* in this study) will likely increase invertebrate abundance and add to the prey base for fish and birds. A management plan based on mechanical control will require a larger labor force than chemical control and it will also require a place to dispose of water hyacinth. Disposal of water hyacinth was a concern expressed by water managers in the state of Jalisco in summer 2006. The concern was over the contaminants retained in the plants that would seep into the ground upon deposition in a landfill. In response to alternative uses of the extracted plant (e.g., paper, biofuel, furniture, baskets, etc.), managers were also concerned with human contact with the plant that might occur at processing facility. The most recent study published in a peer-reviewed journal that quantified contaminant concentrations within plants was conducted in 1990 (Shine *et al.*, 1998). Shine *et al.* (1998) found the highest concentration of metals in the roots. Plant roots had higher concentrations for most metals, and much higher concentration of lead, zinc, nickel, and copper. Further research is needed to ascertain the current toxicity of the water hyacinth plants at Lake Chapala and to determine the potential health risks associated with different degree of contact with the plant.

This study is relevant on a worldwide scale, particularly in aquatic systems outside of water hyacinth's native range where the plant poses a threat. Water hyacinth never covered the entire surface of Lake Chapala like it has in smaller waterbodies worldwide (Navarro & Phiri, 2000; Mangas-Ramirez & Elias-Gutierrez, 2004); therefore, the results of this study are most applicable to similar systems that experience moderate coverage.

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