

Nonlinear and density-dependent fish habitat selection across physiochemical gradients in an invasive macrophyte habitat

Kyle L. Wilson · Micheal S. Allen ·
Robert N. M. Ahrens · Michael D. Netherland

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Abstract Invasive macrophytes drive substantial changes to freshwater fish habitats. Such changes can influence how fish select for habitats, but fish–habitat relationships in many invasive macrophytes are often poorly understood at micro-scales. Fish habitat use is influenced by dissolved oxygen (DO) and habitat complexity, but this response can be nonlinear and dependent upon fish density. This study tested whether micro-habitat use of sunfish (*Lepomis* spp.) in invasive macrophyte beds was density-dependent. Fish were sampled with underwater video point counts in six 0.405 ha experimental ponds with surface-matted hydrilla *Hydrilla verticillata* and stocked with varying densities of sunfishes. Regression models were used to evaluate the key drivers for fish habitat selection across DO, complexity and fish densities. Both fish occurrence and fish counts were positively influenced by DO and negatively influenced by habitat complexity, but the fish counts–

DO relationship was dome-shaped and both fish occurrence and counts depended upon fish densities. For example, at high fish densities, fish used low and high DO and high macrophyte complexity; at low fish densities, fish avoided such areas. Fish counts peaked at intermediate DO and low macrophyte complexity. Density-dependent fish habitat selection appeared to mitigate detrimental effects of invasive macrophytes on fish habitats, indicating that fish can and do use ‘inhospitable’ habitats with potential positive population growth. Understanding density-dependent habitat selection is needed when evaluating the quality of habitats, as apparently inhospitable habitats can be utilized when fish density is high.

Keywords *Lepomis macrochirus* · *Hydrilla verticillata* · Aquatic plant management · Fish–macrophyte relationships · Freshwater fisheries · Underwater video

K. L. Wilson (✉) · M. S. Allen · R. N. M. Ahrens
School of Forest Resources and Conservation, Program of
Fisheries and Aquatic Sciences, University of Florida,
7922 NW 71st St., Gainesville, FL 32653, USA
e-mail: wilsok@ucalgary.ca

M. D. Netherland
US Army Engineer Research and Development Center,
7922 NW 71st Street, Gainesville, FL 32653, USA

Present Address:

K. L. Wilson
Department of Biological Sciences, University of Calgary,
2500 University Drive N. W., Calgary, Alberta,
Canada T2N 1N4

Introduction

Macrophytes produce dissolved oxygen (DO) and structural complexity providing important forage, nursery, and refuge habitats for freshwater fishes (Kramer 1987; Dibble et al. 1996; Caraco et al. 2006). Much of the initial processes assumed to structure fish–macrophyte interactions resulted from assessing bluegill *Lepomis macrochirus* habitat use in native macrophytes in temperate lakes (e.g., Hall and Werner 1977; Gilliam and Fraser 1987; Werner and Hall 1988; Osenberg et al.

1992). However, invasive macrophytes often change fish habitat quality and appear to alter fish habitat selection, sometimes in counterintuitive manners (Lillie and Budd 1992; Chick and McIvor 1994; Peterson et al. 2003; Hershner and Havens 2008). Much of our current understanding of fish habitat use of invasive macrophyte come from coarse and qualitative comparisons in fish assemblages, diets, or behaviours before and after large-scale reductions of invasive macrophytes (Colle and Shireman 1980; Bettoli et al. 1993; Sammons et al. 2003). This is primarily because fish microhabitat use (i.e., point-scale) in invasive macrophytes remains largely unknown due to difficulties sampling fishes in highly complex habitats typical to invasive macrophytes (Dibble et al. 1996; Bayley and Austen 2002; Wilson et al. 2014). As a result, management must often assume that the initial findings of native fish–macrophyte interactions generalize more broadly towards fish habitat use in invasive macrophytes in order to develop control measures for the invasive species (FWC 2011).

Hydrilla *Hydrilla verticillata* is a commonly-managed invasive macrophyte with global distribution that both forage and recreational fishes, such as bluegill, use as habitat (Langeland 1996; Peterson et al. 2003; Barrientos and Allen 2008; Coetzee et al. 2009). Due to high biomass, hydrilla and other invasive macrophytes strongly influence DO dynamics by generally reducing DO underneath surface-matted canopies potentially towards hypoxic levels below $2 \text{ mg}\cdot\text{L}^{-1}$ (Miranda et al. 2000; Colon-Guad et al. 2004; Caraco et al. 2006). Most fish species are sensitive to low DO levels, thus many invasive macrophytes are thought to reduce fish habitat quality (Miranda and Hodges 2000; Killgore and Hoover 2001; Bunch et al. 2010). For example, redear sunfish *L. microlophus* and bluegill, though hypoxia-tolerant, are sensitive to DO-levels below $1.5 \text{ mg}\cdot\text{L}^{-1}$ (Killgore and Hoover 2001), and hydrilla increases the prevalence of hypoxia at depths commonly inhabited by sunfish (Miranda and Hodges 2000; Colon-Guad et al. 2004). Additionally, hydrilla typically increases habitat complexity (Schultz and Dibble 2012), which changes foraging efficiency thereby also influencing fish habitat quality (Crowder and Cooper 1982; Lillie and Budd 1992). Hydrilla appears as a preferred fish habitat in some regard due to high complexity, DO production, and macroinvertebrate densities (Chick and McIvor 1994; Colon-Guad et al. 2004; Barrientos and Allen 2008; Theel et al. 2008), but the processes governing fish habitat selection within hydrilla remain poorly

quantified despite hydrilla's increasing global distribution and demands for management and control (Peterson et al. 2003; Coetzee et al. 2009).

Like many invasive macrophytes, hydrilla influences DO and habitat complexity which are two important measures for fish habitat quality (Miranda et al. 2000; Colon-Guad et al. 2004; Schultz and Dibble 2012). Given that fish habitat selection along habitat quality gradients can be nonlinear (Miranda and Hodges 2000; Dunham et al. 2002), fish responses to gradients in both DO and complexity may be linear or nonlinear. In experiments with open, edge, and densely vegetated habitats available, the fish–habitat complexity relationship appears dome-shaped but this nonlinearity appears partly due to interactions between DO and macrophyte abundance in addition to changes in foraging efficiency and predator encounter rates (Dibble et al. 1996; Miranda and Hodges 2000). Thus, quantifying the shape of this relationship is important to predicting fish responses to changing habitat conditions influenced by commonly-managed invasive macrophytes.

Habitat complexity and DO mediate fish densities and habitat selection (Crowder and Cooper 1982; Kramer 1987; Miranda et al. 2000). Changes in fish densities can dynamically influence fish habitat selection because habitat selection is often density-dependent as individuals compete for space in limited optimal habitat patches (Fretwell and Lucas 1970; Morris 1987). Specific instances of density-dependent habitat selection (DDHS) have been frequently observed in terrestrial animals but less so in fish populations, particularly of freshwater fishes (Bult et al. 1999; Lindberg et al. 2006). Hence, any assessment of fish habitat selection across habitat quality gradients in invasive macrophytes should take into account fish densities (Dunham et al. 2002). However, fish densities in invasive macrophytes have been difficult to estimate due to the aforementioned sampling problems in complex habitats. Recent methodological developments allow for underwater cameras to estimate relative fish density in dense invasive macrophytes from point-count sampling (Wilson et al. 2014). The objectives of this study were to use underwater cameras to evaluate fish habitat selection in hydrilla by: 1) quantifying point-scale sunfish habitat use patterns across DO and habitat complexity gradients under in situ conditions, 2) assessing whether habitat use varied with fish density, and 3) determining whether fish–habitat quality patterns along these gradients were linear or nonlinear. Such findings can improve the

current understanding of optimal fish habitat conditions when managing invasive macrophyte beds.

Methods

Study site and sampling

Sampling occurred in six rectangular 0.405 ha experimental ponds (maximum depth 2.4 m, average depth 1.7 m) located at a United States Geological Survey facility in Gainesville, Florida. Three ponds were sampled from July to September 2011 (for details on 2011 ponds, see Wilson et al. 2014) and three additional ponds were sampled from July to August 2012 (Table 1). Ponds were filled from the same source of well-water and water temperatures ranged from 24 to 28 °C, typical for subtropical lakes in Florida during late summer. All six ponds had ~100 % coverage of surface-matted hydrilla by mid-June (no other macrophyte species were present) and remained at 100 % surface coverage until the ponds were drained in October of each year. Each pond was aerated continuously with an aerator located above the deepest portion of the pond (i.e., the catch basin) to create a gradient for DO levels decoupled from habitat complexity and hydrilla biomass. Due to the artificial control of the initial environmental conditions of each pond, the initial abundance of natural prey items for *Lepomis* spp. (e.g., macroinvertebrates such as Odonata) was assumed constant across all

ponds. Aquatic plant biomass was sampled ($\text{kg}\cdot\text{m}^{-2}$ in dryweight) from four to seven random locations each month using boat-based vertical rakes (Johnson and Newman 2011).

Fish densities were manipulated among ponds by varying stocking abundances (Table 1). In June 2011, Pond 1 was stocked with 75 adult (>140 mm TL total length) *Lepomis* spp. (bluegill and redear sunfish), Pond 2 was stocked with 150 adult *Lepomis* spp., and Pond 3 had an established multi-year fish community assumed to be at a high-capacity equilibrium with high densities of *Lepomis* spp. and a remnant population of three adult largemouth bass *Micropterus salmoides*. This equilibrium assumption was supported in prior analyses of the 2011 ponds (Wilson et al. 2014). In June 2012, Ponds 4, 5, and 6 were all stocked with 200 adult *Lepomis* spp. (both bluegill and redear sunfish). Size distributions were similar for all stocked ponds. Bluegill comprised 70–80 % of all stocked fish while redear sunfish comprised the rest. Bluegill and redear sunfish were selected as these two *Lepomis* spp. represent economically-valuable recreational fishes, provide important ecological structure, co-occur in macrophyte beds across Florida lakes, and their heterospecific interactions towards one another have not been shown to be antagonistic (Colle and Shireman 1980; Martin et al. 1992; Bachmann et al. 1996; VanderKooy et al. 2000). After stocking, the ponds were not manipulated and fish populations were allowed to persist under the relatively natural conditions afforded by the ponds. Competition

Table 1 Habitat and fish characteristics of six 0.405 ha ponds used to measure fish habitat use of 100 % surface-matted hydrilla

Year	Pond	Starting abundance	End-of-season abundance	DO ($\text{mg}\cdot\text{L}^{-1}$)	Hypoxia prevalence	Habitat complexity	Hydrilla biomass ($\text{kg}\cdot\text{m}^{-2}$)
2011	1*	75	21	2.37 a	0.33 a	70 % a	1.57 a
2011	2*	150	5063 (3972–6155)	2.35 a	0.4 a	55 % b	3.11 a
2011	3*	Carrying capacity	15,387 (12,445–18,330)	2.51 a	0.33 a	69 % a	2.79 a
2012	4	200	11,831 (19,829–13,832)	2.86 a	0.38 a	73 % a	2.11 a
2012	5	200	21,520 (19,171–23,869)	2.53 a	0.34 a	57 % a,b	1.55 a
2012	6	200	16,670 (14,163–19,177)	2.08 a	0.45 a	69 % a	3.81 a

Descriptions include: stocking abundance in June of each year, estimated end-of-season abundance as sampled after draining each pond (with associated 95 % confidence intervals in parentheses), as well as mean dissolved oxygen (DO) levels, hypoxia prevalence (proportion of sites with $\text{DO} < 1.5 \text{ mg}\cdot\text{L}^{-1}$), mean habitat complexity, and mean hydrilla biomass ($\text{kg}\cdot\text{m}^{-2}$ dryweight) during the sample season. Significant groupings detected by Tukey HSD pairwise comparisons denoted by lowercase letters. Carrying capacity assumption in Pond 3 supported by analyses in Wilson et al. 2014. Ponds with * were assessed in Wilson et al. 2014 which evaluated the methodology of using underwater video to track true fish population abundances in hydrilla

for available resources after stocking was assumed to be influenced by fish density and not by variation in initial prey abundance.

Underwater video cameras (UVC) were used to repeatedly measure in situ fish habitat use by conducting 10–20 point counts every 2 to 4 weeks at random locations in each pond (video methods detailed in Wilson et al. 2014). The area sampled by video camera ranges from 0.5 to 1.0 m² and does not vary substantially with habitat complexity (Wilson 2013; Wilson et al. 2014). For each sample week, both the starting pond and starting sample location were random such that, for example, early-morning sampling did not consistently occur nearest the aerator. Samples were taken from July through September in 2011, and from July through August in 2012. Video samples could only be taken during daylight hours (9:00 to 17:00) to ensure sufficient light for the UVC. For each video point count, the UVC was lowered from a 3.6 m flat-bottom boat and through the hydrilla canopy layer. The boat was maneuvered around the ponds to random locations with paddles. This sampling approach had no significant bias on fish behavior and video duration did not affect the expected arrival time of the maximum number of fish (see Wilson et al. 2014). Before recording, the UVC field-operators ensured the camera's field-of-view was not overly obstructed by vegetation and then recorded video for five to ten minutes. This sampling design was used to collect presence-absence (hereafter called occurrence) and count fish abundance beneath the hydrilla surface canopy layer in each pond. Immediately after video recording at each point, DO (mg·L⁻¹) was collected in the field-of-view of the camera (i.e., in the same location of the on-camera fish) using a handheld YSI 556MPS dissolved oxygen meter. The random locations and random starting point of the sample locations during each sample week on each pond minimized spatial autocorrelation of fish and habitat samples (Wilson et al. 2014).

Fish occurrence, fish counts, and habitat complexity were measured from video analysis of each point count, thus fish occurrence and fish counts were measured for all fish (both young-of-year and adult) at a point-scale resolution (example in Fig. 1). Fish detection rates with UVC sampling were relatively high (>65 % detection probability) and constant across ponds and habitat complexity (Wilson 2013; Wilson et al. 2014). If fish were observed at any time during video fish were noted as present, otherwise fish were considered absent. When

fish were present, individuals were counted with the *MaxN* metric, the maximum number of individual fish onscreen at any one time during video sampling (Wilson et al. 2014). The use of the *MaxN* metric precluded the possibility of double-counting mobile individuals during a point count. For each UVC point count, habitat complexity was measured as the percent of macrophytes covering the screen from 0 to 100 %. For each point count, a single 640×480 resolution frame was captured from video and the image was divided up into a grid of 56 equal-sized squares. Video observers counted the number of squares of the grid >50 % covered by vegetation (considered 'vegetated') and the number of squares <50 % covered by vegetation (considered 'open'). For example, a habitat with 50 'vegetated squares' out of 56 had 89 % complexity and was considered highly complex. If fish were present, habitat complexity was measured at the time interval where the maximum number of fish occurred; if fish were absent, habitat complexity was measured at a time interval that best represented the duration of the video.

Seasonal abundances of *Lepomis* spp. can fluctuate two- to five-fold during a single season (Hall and Werner 1977). Analyses for density-dependent habitat selection needed to account for potential seasonal changes in fish density. Mean *MaxN* per sample week was found to track true population densities very efficiently in Wilson et al. (2014). We calculated the mean *MaxN* per sample week and categorized fish density according to a natural range of fish densities in vegetated Florida lakes (Bachmann et al. 1996). In this, a *MaxN*<1 was categorized as low fish density (corresponding to ~6000 fish·ha⁻¹ or 55 kg·ha⁻¹); $1 \leq \text{MaxN} < 2.25$ was medium-low; $2.25 \leq \text{MaxN} < 3.5$ was medium-high; and *MaxN*≥3.5 was high fish density (corresponding to ~40,000 fish·ha⁻¹ or 340 kg·ha⁻¹).

All ponds were drained in October of their sample year and a combination of netting and quadrat sampling was used to estimate the true total fish population size at the end of the pond manipulations. After the ponds drained, most fish moved to the 'catch basin' (~5.0 m² in area) and were collected with hand nets; the 'catch basin' is an area at the deepest portion of the pond near the drain that screens fish from outflowing water. The perimeter of the pond was then surveyed to measure the total pond area that still contained fish caught in the dense vegetation. This area of the pond was then sampled with 25–30 randomly-placed quadrats (0.25 m²) to sample for any fish still outside of the catch basin. Fish



Fig. 1 Redear and bluegill sunfish (maximum number of individuals counted, $MaxN=10$) inhabiting a location with dissolved oxygen levels at 0.95 mg L^{-1} (defined as hypoxic) and 39 % habitat complexity in a high fish density pond with 100 % surface-coverage of hydrilla during 2011

were identified by taxon and the quadrat samples were analyzed in a negative binomial log-likelihood structure to obtain maximum likelihood estimates (MLE) of the total fish population outside the catch basin. The MLE 95 % confidence intervals were calculated for each pond using $\pm$ the t statistic multiplied by the standard error of the MLE. The MLE for the total numbers of fish outside of the catch basin was then added to the total numbers of fish removed from the catch basin to obtain a final MLE of total fish population size per taxa in each pond with associated 95 % confidence intervals.

Statistical analyses

Analysis of Variance (ANOVA) and Tukey HSD pairwise comparisons ($\alpha=0.05$) in Program R were used to assess whether habitat conditions such as hydrilla biomass, DO levels, and habitat complexity differed across the six ponds (R Development Core Team 2013). Linear regression was then used to evaluate whether DO was influenced by habitat complexity to determine if the two measures of habitat quality were decoupled and independent or if further tests should account for an interaction between DO and habitat complexity. Chi-square tests of equal proportions were used to determine if the prevalence of hypoxia (i.e., proportion of total sample sites with $<1.5 \text{ mg}\cdot\text{L}^{-1}$) varied

across the six ponds and across the four fish density categories, and whether fish use of hypoxic sites varied across fish density.

Simple regression analyses are useful tools in evaluating tests of DDHS theory across varying animal densities and habitat qualities (Morris 1987). Generalized linear models (GLM) were used to evaluate if point-scale fish occurrence and fish counts within all ponds were influenced by fish density, DO and habitat complexity ($\alpha=0.05$). In this case, relative fish density was taken as the mean $MaxN$ for the sample week, continuous covariate, and not the density categories as before. Fish occurrence was modeled with a logit-transformed logistic regression while fish counts were modeled with a negative-binomial regression using the function ‘glm.nb’ in the Program R MASS package (Venables and Ripley 2002). The negative binomial regression is widely used in animal ecology to understand the relationship between animal count data and environmental conditions (Ver Hoef and Boveng 2007; Yokota et al. 2009), and was chosen due to overdispersion in the count data compared with initial analyses using a Poisson distribution.

We evaluated and ranked several candidate regression models (both occurrence and count models; Table 2) using Akaike’s Information Criterion (Akaike 1974) corrected for small sample size (AIC_c). In these models, we varied the coefficients to include: 1) fish density; 2) strictly linear effects of DO and habitat complexity; 3) nonlinear effects of either or both DO and complexity using a 2nd order polynomial, and 4) an interaction between DO and habitat complexity. Models with ΔAIC_c values of <10.0 have moderate support and <2.0 have substantial support and are considered equivalent at explaining the data; if models were equivalent (i.e., the two models were differentiated by $<2.0 \Delta AIC_c$) we selected the model with the highest weighted AIC_c (w_i) calculated as:

$$w_i = \exp(-0.5 \times \Delta AIC_c i) / \sum_{r=1}^R \exp(-0.5 \times \Delta AIC_c r) \quad (1)$$

where R is the number of regression models ranked according to Burnham and Anderson (2004). Pearson’s chi-squared goodness-of-fit tests were conducted to assess the fit of the AIC-selected fish occurrence and fish count regression models compared with an intercept-only null model, a fish density-only null model, and a

habitat-only null model. Since R^2 goodness-of-fit measures are not generalizable across many count regression models (Cameron and Windmeijer 1996), we further assessed goodness-of-fit by comparing the frequency of fish counts estimated by the AIC-selected model to the observed fish count frequency (e.g., Yokota et al. 2009), and by comparing both the ratio of the residual deviance to the degrees of freedom and the Pearson goodness-of-fit χ^2 value to the degrees of freedom; both ratios should approach 1 for good-fitting models of count data (Allison and Waterman 2002). Results from AIC-selected logistic regression for predicted fish occurrence were compared with a histogram of habitat data according to recommendations of Smart et al. (2004) using modifications to the ‘popbio’ package in Program R (Stubben and Milligan 2007).

Point-scale animal count data from repeated measures are often spatially autocorrelated leading to pseudo-replication and inflated degrees of freedom for statistical tests of animal–habitat relationships (Diniz-Filho et al. 2003). This concern was addressed via analyses conducted in Wilson et al. (2014) where the efficacy of using underwater video cameras to sample fish counts in macrophytes was verified, and spatial-autocorrelation and the double-counting of individuals was not found to bias statistical inference. Further, the negative binomial regression has relaxed assumptions to violations of sample independence (e.g., due to double-counting mobile individuals between sample sites), and autocorrelation does not inherently lead to increased Type-I error nor bias statistical results made by regression analyses fit with least square residuals, such as the iteratively reweighted least square residual used in the ‘MASS’ package (Venables and Ripley 2002; Diniz-Filho et al. 2003).

Results

Habitat conditions

Habitat characteristics such as DO, complexity and hydrilla biomass varied, but not very significantly, across the six ponds (Table 1). Hydrilla was prolific across all six ponds with 100 % surface coverages from June through October in each year in each pond, and mean hydrilla biomass ranging from 1.55 to 3.81 kg·m⁻² dryweight (dwt). Differences in hydrilla biomass across the six ponds was weakly significant (ANOVA F

value=2.67, degrees of freedom (d.f.) = 5, 60, $p=0.03$) but Tukey HSD pairwise comparison detected no significant groupings among the ponds with the largest difference as the 2.24 difference in kg·m⁻² dwt difference between pond 1 and pond 6 (all pairwise comparisons $p>0.05$). Dissolved oxygen did not vary significantly across the six ponds (ANOVA $F=1.03$, d.f.=5365, $p=0.4$) with mean DO ranging from 2.08 to 2.86 mg·L⁻¹, all at intermediate hypoxia levels for bluegill and redear sunfish according to Killgore and Hoover (2001). Habitat complexity was intermediate to high with mean complexity ranging from 55 to 73 %. Complexity significantly differed across the six ponds (ANOVA $F=4.98$, d.f.=5, 365, $p=0.002$) and Tukey HSD detected significant groupings with ponds 1, 3, 4, 5, and 6 in group *a* and ponds 2 and 5 in group *b* (Table 1). Dissolved oxygen and habitat complexity were not significantly related (Linear regression $F=3.10$, d.f.=1, 369, $p=0.08$), but indicated a potential, mild statistical interaction that was further tested in nested AIC models. The prevalence of hypoxia was not different across the six ponds (Proportions test $\chi^2=2.62$, d.f.=5, $p=0.76$) with the proportion of hypoxia sites ranging from 0.32 to 0.45. The prevalence of hypoxic conditions was significantly, positively related with habitat complexity (ANOVA $F=1072$, d.f.=2, 369, $p<<0.001$). Hypoxia occurred throughout a range of habitat complexities from 18 to 100 %, however habitat complexity ≥ 71 % was associated with increased hypoxic conditions while habitat complexity ≤ 61 % was associated with increased normoxic conditions.

Fish abundances in ponds

True fish abundances varied across the six ponds (Table 1). The areas outside the catch basin still containing fish after drainings (i.e., the total area sampled with quadrats) also varied among ponds with pond 1’s area at 203 m², pond 2’s at 675 m², pond 3’s at 1350 m², pond 4’s at 675 m², pond 5’s at 675 m², and pond 6 at 810 m². The starting and ending abundances in each pond indicated that substantial population growth of sunfish populations occurred in ponds 2, 4, 5, and 6. Every pond except for pond 1 achieved intermediate to high fish densities by the end-of-season pond drainings. Pond 3 contained only three adult largemouth bass (fish >300 mm TL) and an estimated 700 juvenile largemouth bass sized 80–120 mm TL (95 % CI 67–1478 fish), substantially lower than average bass densities in

Florida lakes according to Bachmann et al. (1996). For subsequent analyses, all fish species were combined together since juvenile largemouth bass were not abundant and were present only in Pond 3, the juvenile bass were not at a size for piscivory (Bettoli et al. 1992) and small, juvenile bass show similar habitat associations and DO requirements as sunfishes (Miranda et al. 2000; Killgore and Hoover 2001).

Relative fish density estimated from *MaxN* changed during the sample season. Fish occurred in 62 % of all samples and a total of 371 fish point-counts were collected in dense hydrilla across the six ponds: 256 in 2011 and 115 in 2012. The 2011 ponds were sampled from July through September, and mean *MaxN* in pond 1 changed from 0.35 in July, to 0.07–0.38 in August, and 0.25–1.10 in September. This qualified pond 1 densities as mostly low to medium-low in density. Mean *MaxN* in pond 2 changed from 0.11 in July, to 0.45–1.15 in August, and 2.33–3.74 in September. This qualified pond 2 densities as changing from low to high fish densities over the sample season. Mean *MaxN* in pond 3 changed from 4.75 in July, to 4.00–4.15 in August, and 5.19 in September. This qualified all of pond 3 as high density. The 2012 ponds were only sampled July and August. Mean *MaxN* in pond 4 changed from 2.25 in July to 1.80 in August. Mean *MaxN* in pond 5 changed from 5.80 in July to 2.47 in August. Lastly, mean *MaxN* in pond 6 changed from 0.70 in July to 2.20 in August. This qualified all of pond 4 as medium-low density, pond 5 as changing from high to medium-high density, and pond 6 as changing from low to medium-low density.

Fish use of hypoxia

Fish utilization of hypoxic habitats was density-dependent. The proportion of hypoxic locations, defined as locations with DO levels $< 1.5 \text{ mg} \cdot \text{L}^{-1}$, did not vary across the six ponds (Table 1). However, hypoxia occurred more frequently in low density ponds and was negatively related to fish density with the lowest prevalence of hypoxia in high density ponds (Table 2; proportions test $\chi^2=8.67$, d.f.=3, $p=0.03$). Despite the reduced prevalence of hypoxia in high and medium-high density, fish occurrence within hypoxic locations increased with fish density (Table 2; proportions test $\chi^2=67.42$, d.f.=3, $p<<0.001$). Sunfish avoided hypoxic locations when

densities were low, but utilized hypoxic habitats at high fish densities.

Fish habitat selection along habitat gradients

There was strong evidence for density-dependent fish habitat selection across the DO and habitat complexity gradients. Fish occurrence was significantly influenced by fish density, DO, and habitat complexity (Table 3; logistic regression null deviance = 514.32, residual deviance = 264.81, d.f.=3, 368, $p<<0.001$). The AIC-selected logistic regression showed positive linear effects of fish density and DO on fish occurrence (both $p<0.001$; Fig. 2a), and a negative effect of habitat complexity ($p<0.001$; Fig. 2b):

$$\text{Occurrence} = 0.29 \times \text{DO} - 3.14 \times \text{Complexity} + 1.30 \times \text{Density} \quad (2)$$

indicating that fish occurrence within hydrilla habitats were influenced both by population density and habitat qualities. A histogram of the logistic regression suggests relatively high goodness-of-fit (Fig. 2c). Pearson's chi-squared likelihood ratio tests of the AIC-selected logistic regression further showed high goodness-of-fit when compared to an intercept-only null model ($\chi^2=249.51$, d.f.=3, $p<<0.001$), a density-only null model ($\chi^2=99.71$, d.f.=2, $p<<0.001$), and a habitat-only null model (DO and complexity as linear effects; $\chi^2=173.13$, d.f.=1, $p<<0.001$).

Fish counted across habitat quality gradients were significantly density-dependent but also showed nonlinear responses to habitat quality. Fish counts were significantly influenced by fish density, DO, and habitat complexity (Table 3; negative binomial regression null deviance = 1123.03, residual deviance = 358.05, d.f.=5, 366, $p<<0.001$). The AIC-selected negative binomial regression showed a positive linear effect of fish density ($p<<0.001$; Fig. 3), a positive nonlinear effect of DO ($p<<0.001$; Fig. 3a), a negative linear effect of habitat complexity ($p<<0.001$; Fig. 3b), and weak interaction between DO and habitat complexity on fish counts ($p=0.082$; Fig. 3):

$$\begin{aligned} \text{Counts} = & 0.27 \times \text{DO} - 0.05 \times \text{DO}^2 - 1.95 \\ & \times \text{Complexity} + 0.14 \times \text{DO} \\ & \times \text{Complexity} + 0.49 \times \text{Density} \end{aligned} \quad (3)$$

suggesting that local fish abundances within hydrilla

Table 2 Hypoxia prevalence (proportion of sites with DO <1.5 mg·L⁻¹) and proportion of fish occurrence within hypoxic sites across fish density categories

Fish density	Hypoxia prevalence	Fish occurrence in hypoxia
Low (140)	0.44	0.16
Medium-low (90)	0.39	0.49
Medium-high (27)	0.30	1.00
High (114)	0.27	1.00

Number of sample sites for each category shown in parentheses. Fish densities estimated from mean maximum number of individuals counted from video point counts and categorized according to natural gradient of fish densities in Florida lakes following Wilson et al. (2014)

habitats were influenced both by population density and habitat quality and the response was dome-shaped. Comparisons of the observed and estimated fish count frequencies suggested relatively high goodness-of-fit (Fig. 3c). The ratio of the residual deviance (358.05) to the degrees of freedom (371) was 0.97 and the ratio of Pearson goodness-of-fit χ^2 value (414.48) to the degrees of freedom was 1.12. Both ratios were close to 1.0 and suggested high goodness-of-fit (Allison and Waterman 2002). Pearson's chi-squared likelihood ratio tests of the AIC-selected negative binomial regression further showed high goodness-of-fit when compared to an intercept-only null model ($\chi^2=414.48$, d.f.=5, $p<<$

0.001), a density-only null model ($\chi^2=143.49$, d.f.=4, $p<<0.001$), and a habitat-only null model (DO and complexity as linear effects; $\chi^2=281.4$, d.f.=3, $p<<0.001$).

Fish occurrences and fish counts did not always strongly respond to changes in habitat quality metrics but this depended on fish density. Fish occurrence in high fish densities was flat across the DO and habitat complexity gradients (Fig. 2a, b) indicating that fish occurrence may signal fish habitat quality at high densities. In low fish densities, fish occurrence responded strongly to habitat quality as fish occurred most often in areas of high DO and low complexity, avoiding low DO

Table 3 Relative ranking of the tested regression models for fish habitat selection within hydrilla habitats including linear and non-linear effects (modeled as a 2nd order polynomial) for fish counts, using a negative binomial regression, and fish occurrence, using a logistic regression, according to AIC_c and weighted AIC_c (w_i)

Model	# par	AIC _c	Δ AIC _c	w_i
Negative binomial regression models				
Density + DO × Complexity + DO ²	5	1150.835	0.000	0.404
Density + DO + PAC + DO ²	4	1151.661	0.826	0.267
Density + DO × Complexity + DO ² + Complexity ²	6	1152.377	1.542	0.187
Density + DO + Complexity + DO ² + Complexity ²	5	1153.727	2.892	0.095
Density + DO + Complexity	3	1156.153	5.318	0.028
DO + Complexity + Complexity ² + Density	4	1157.726	6.891	0.013
Density + Complexity	2	1159.194	8.359	0.006
Density + DO	2	1283.270	132.435	0.000
Logistic regression models				
Density + DO + Complexity	3	270.873	0.000	0.477
DO + Complexity + Complexity ² + Density	4	272.712	1.839	0.190
Density + DO + PAC + DO ²	4	272.917	2.044	0.172
Density + DO + Complexity + DO ² + Complexity ²	5	274.730	3.857	0.069
Density + DO × Complexity + DO ²	5	274.938	4.065	0.062
Density + DO × Complexity + DO ² + Complexity ²	6	276.786	5.913	0.025
Density + Complexity	2	279.836	8.963	0.005
Density + DO	2	361.338	90.465	0.000

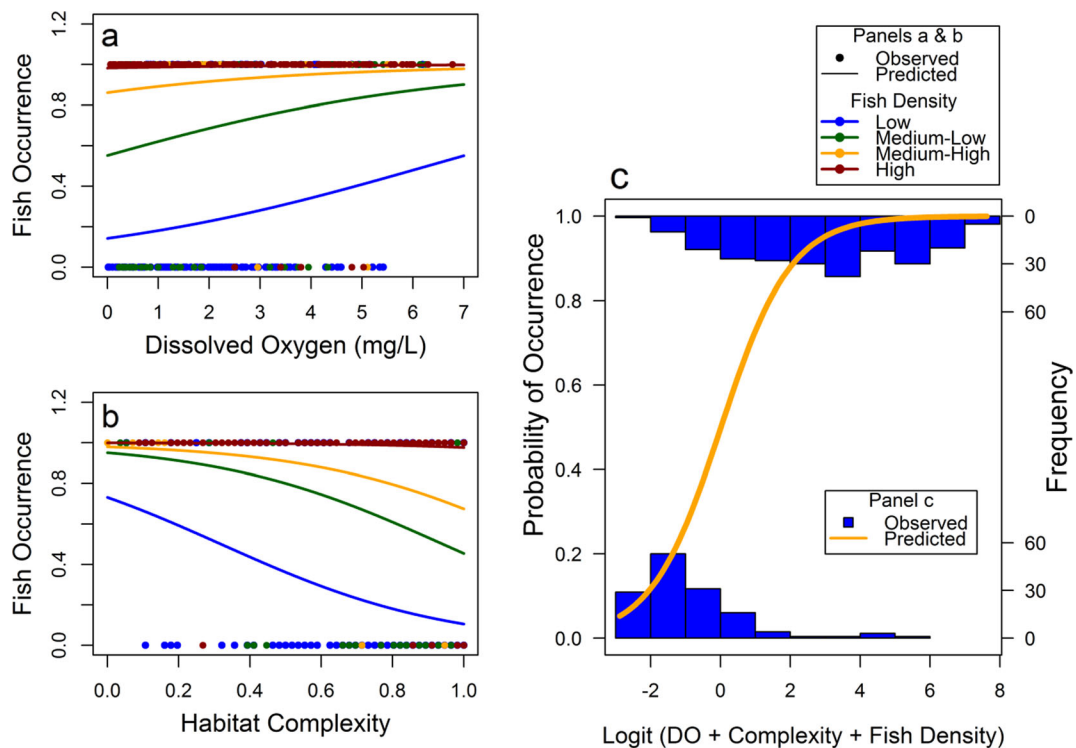


Fig. 2 Observed and predicted fish occurrence in hydrilla habitats along a gradient of dissolved oxygen (DO) and habitat complexity across four fish densities: low, medium-low, medium-high, and high (panels **a** and **b**). The relative goodness-of-fit for the AIC-

selected logistic regression shown with a histogram of logit-transformed habitat data compared with associated probability of fish occurrence (panel **c**)

and highly complex habitats. Patches with high DO and low complexity generally increased fish occurrence but only at low to intermediate fish densities (Fig. 4). Conversely, fish counts in high fish densities showed a strong, nonlinear signal across the DO gradient (Fig. 3a) and a linear signal across habitat complexity gradients (Fig. 3b) suggesting a positive relationship between fish counts and fish habitat qualities at higher fish densities. In low fish densities, fish counts did not respond strongly to habitat quality gradients. Results from the fish count model suggest that fish abundances peaked just above hypoxic conditions $\sim 2\text{--}4$ DO $\text{mg}\cdot\text{L}^{-1}$ and in low complexity but changed with fish densities (Fig. 5).

Discussion

Freshwater fish habitat selection in invasive macrophytes under in situ conditions has rarely been

quantified at micro-scales (Dibble et al. 1996). Our results showed strong evidence for nonlinear density-dependent fish habitat selection (DDHS) across habitat quality gradients driven by hydrilla (Schultz and Dibble 2012). Overall, fish use of hypoxic and other low-quality habitats was density-dependent and fish increasingly used low-quality habitats at high fish densities likely because competition increased. Density-dependent processes showed that fish occurrence did not indicate habitat quality at high total densities but fish counts did. Conversely, the fish counted–habitat quality relationship was flat at low total densities showing that fish counts did not indicate habitat quality. The environmental conditions under which fish densities were manipulated and the decoupled DO–habitat complexity relationship allows these results to readily apply towards optimally managing for fish habitat quality in hydrilla beds, an invasive macrophyte with increasing distribution across North and Central America, Australia, and Africa (Langeland 1996; Peterson et al. 2003; Coetzee et al. 2009).

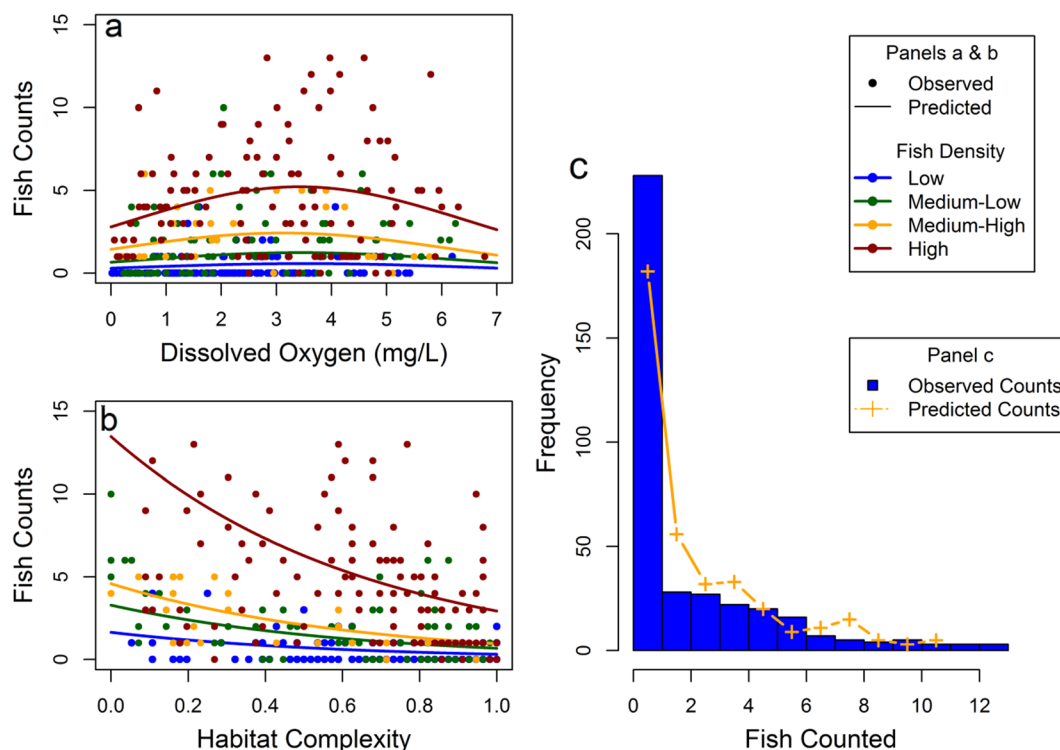


Fig. 3 Observed and predicted fish counts in hydrilla habitats along a gradient of dissolved oxygen and habitat complexity across four fish densities: low, medium-low, medium-high, and

high (panels **a** and **b**). The relative goodness-of-fit for the AIC-selected negative binomial regression shown with a histogram of observed fish counts compared to predicted fish counts (panel **c**)

Sunfish populations can thrive under habitat conditions influenced by hydrilla that are widely considered suboptimal. Hypoxic conditions were common, occurring in 37 % of all locations, and mean DO was near the range sensitive for sunfish according to Killgore and Hoover (2001). Furthermore, macrophyte complexity was at or above intermediate ranges associated with optimal sunfish habitat (Miranda and Hodges 2000), and hydrilla biomass in all six ponds was higher than Florida lakes reported in Bowes et al. (1972) where the highest hydrilla biomass was $0.89 \text{ kg} \cdot \text{m}^{-2}$ in dryweight. For the purposes of fisheries management, these types of environments indicate poor fish habitat quality (FWC 2011). Despite these suboptimal conditions, the population sizes for five of the six ponds achieved or exceeded expected fish densities for Florida's vegetated lakes where fish densities can average $\sim 30,000 \text{ fish} \cdot \text{ha}^{-1}$ (Chick and McIvor 1994; Bachmann et al. 1996). We suggest that density-dependent habitat selection caused hypoxia-tolerant sunfish to use low-quality habitats due to competition for high-quality microhabitats and this increased distribution of occupied habitats allowed

sunfish populations to grow in what would otherwise be adverse conditions.

Hypoxic conditions strongly influenced sunfish habitat use. Once past stressful hypoxic conditions, sunfish appeared to determine habitat quality based on other attributes due to little biological consequence of low, but not hypoxic, DO levels. For example, sunfish seemed to select habitats based more for the location's complexity than DO once past the hypoxic threshold despite interactions between habitat complexity and DO. We do not imply that DO should be kept to intermediate levels for the purposes of managing fish habitats within hydrilla beds. Killgore and Hoover (2001) found that fish species richness is positively correlated with DO. Therefore, a more diverse and resilient fish community may tend to be found in areas with higher DO levels. However, a diminishing return was evident and increases in DO levels did not necessarily lead to increased fish habitat quality which is consistent with Killgore and Hoover (2001) who described this relationship as asymptotic with species richness maximized $\sim 4.0 \text{ mg} \cdot \text{L}^{-1}$. We suggest that some

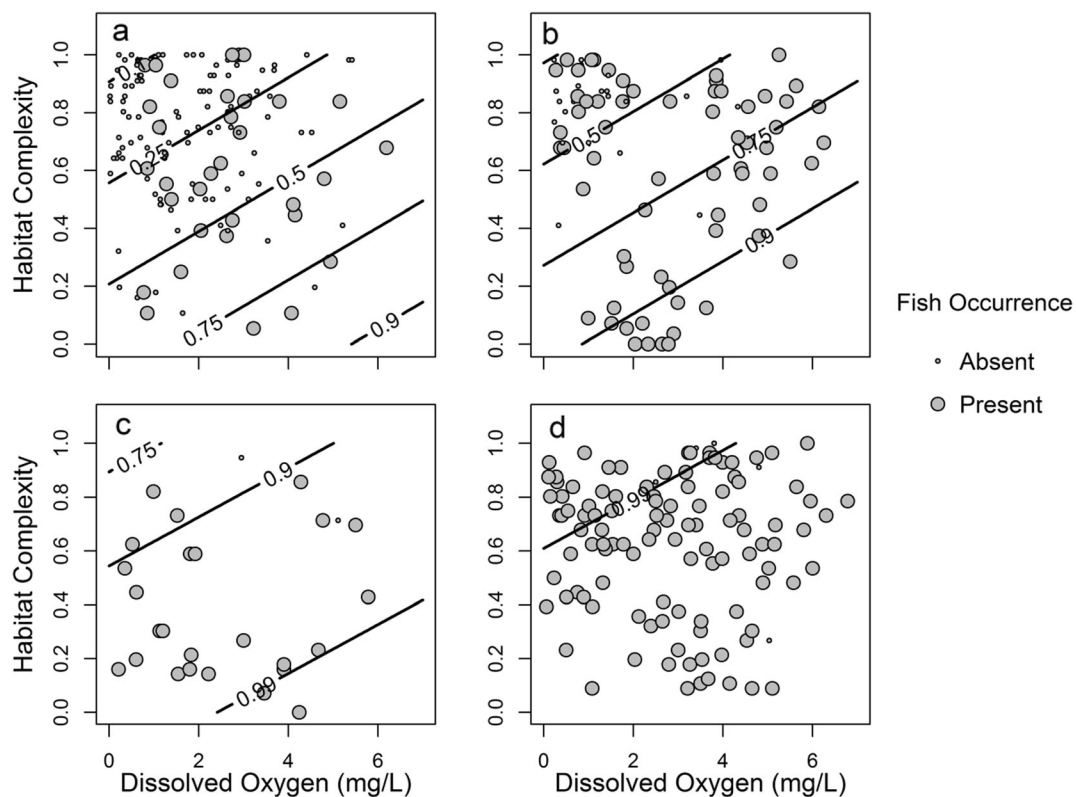


Fig. 4 Contour plot showing the linear effects of habitat complexity and dissolved oxygen ($\text{mg}\cdot\text{L}^{-1}$) on the probability of fish occurrence (from 0.00→1.00) at low, medium-low, medium-high,

and high fish densities (panels **a**, **b**, **c**, **d** respectively) with observed fish occurrences (*grey dots*)

recreationally and ecologically important fishes, such as sunfish, may not respond as strongly to low DO-levels as previously assumed indicating that suitable sunfish habitats can occur across a broader range of DO and complexity. This can be used to guide species-specific regulations and calls for invasive macrophyte control and restoration of native fish habitats (FWC 2011).

The linear response of fish and habitat complexity in this study challenge previous findings between fish and complexity. The findings in this study occurred in ponds with 100 % vegetation, hence truly ‘open’ habitats with low complexity might not have been available unlike in previous fish–complexity studies which showed a dome-shaped relationship (Dibble et al. 1996; Miranda and Hodges 2000). Therefore, our measurement for habitat complexity may be along the linear decline from intermediate to high, and we were only assessing fish along the right hand side of the classic relationship. This linear effect between fish and complexity could

also be a result of very low visual encounters with predators. Only pond 3 held sunfish predators (largemouth bass), and even this was at very low bass density in comparison to Bachmann et al. (1996). Without visually encountering predators, sunfish may select for less complex environments to selectively feed off large macroinvertebrates (Diehl 1992). Further, Savino and Stein (1982) found that visual predator encounters appear to structure prey habitat selection suggesting that, in predator-less environments, the dome-shaped relationship with complexity may not persist. Lastly, the positive association between high habitat complexity and hypoxia also likely reduced sunfish preference for high habitat complexity. Since bluegill and readear sunfish tended to avoid hypoxic areas at low densities, this might have led to the negative relationship between fish and complexity. Future designs should manipulate the patch-mosaic of invasive macrophyte habitats within experimental ponds

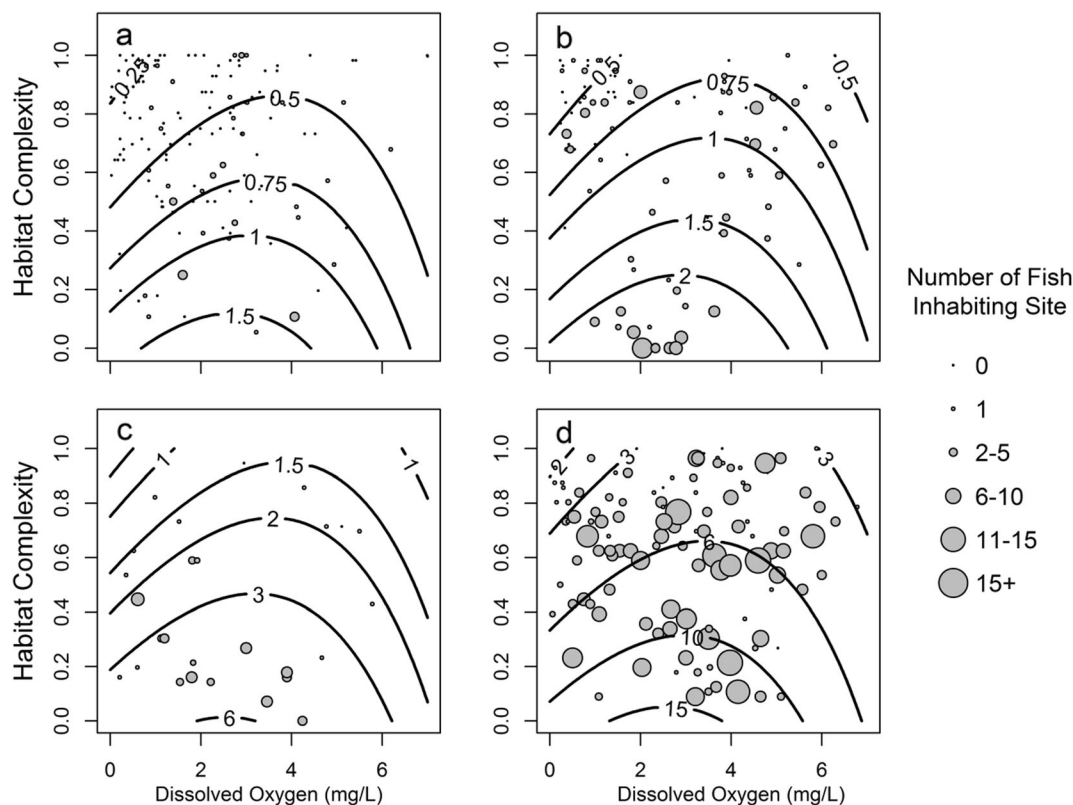


Fig. 5 Contour plot showing the nonlinear, dome-shaped effect of dissolved oxygen (DO; $\text{mg}\cdot\text{L}^{-1}$) and the linear effect of habitat complexity controlling for the interaction between DO and

complexity on fish counts (from 0→15 individuals) at low, medium-low, medium-high, and high fish densities (panels a, b, c, d respectively) with observed fish counts (grey dots)

to broaden the habitat complexity gradient to include truly ‘open’ environments, and continue exploring the interaction between complexity and hypoxia.

The nonlinear relationship between sunfish and DO appears supported from previous fish–macrophyte studies (Miranda et al. 2000). Although DO levels strongly influence habitat use in many fishes (Kramer 1987), increases in DO are not always associated with increases in fish abundance (Miranda and Hodges 2000). Furthermore, DO can be patchily distributed in macrophyte beds with normoxic microhabitats adjacent to hypoxic microhabitats (Miranda et al. 2000). Miranda et al. (2000) found that micro-scale patchiness facilitates fish survival within inhospitable macrophyte beds, and our study also supports that DO patchiness facilitated fish use and population growth within similar environments. Fish subjected to limited optimal habitats will modify habitat selection to minimize the risk to growth ratio termed the ‘minimize μ/f hypothesis’ (Gilliam and

Fraser 1987). We posit that the dome-shaped relationship between sunfish and DO may result from $\text{DO} < 1.5 \text{ mg}\cdot\text{L}^{-1}$ representing a physiological risk, with $\text{DO} > 1.5 \text{ mg}\cdot\text{L}^{-1}$ being suitable for sunfish, while $\text{DO} > 4 \text{ mg}\cdot\text{L}^{-1}$ potentially increases predator encounters (e.g., largemouth bass; Burleson et al. 2001) or becomes a physiological stressor due to difficulties acclimating to highly variable DO environments (Miranda et al. 2000). In environments where DO varies from hypoxia → mild hypoxia → normoxia, sunfish appeared to perceive this gradient as risky → suitable → risky consistent with Miranda et al. (2000).

Density-dependent habitat use by fish has seldom been quantified under natural conditions, especially in freshwater fishes (but see examples in Bult et al. 1999 and Dunham et al. 2002). Eby et al. (2005) found that fish in DO-limited habitats avoided hypoxic areas and tended to overcrowd in high DO habitats leading to density-dependent impacts to growth and survival. Habitat manipulations for Gag grouper *Mycteroperca*

microlepis found that DDHS and limited high-quality habitat regulates growth, survival, and foraging dynamics thus governing fishery production (Lindberg et al. 2006). In this study, sunfish preferred patches of low habitat complexity and high DO and avoided hypoxia, but these habitats were not always available. Unlike Eby et al. (2005), fish in our study sometimes inhabited hypoxic locations, but only at higher population densities. This was likely to avoid higher fish densities that could restrict per-capita resource intake or attract predators towards overcrowded patches. Competition for limited resources can increase mortality as fish adopt risk-taking behaviours at higher densities (Gilliam and Fraser 1987). Increased population densities seemed to influence sunfishes' perception of optimal and suboptimal habitats, and these species' hypoxia-tolerance (Killgore and Hoover 2001) may have allowed them to use lower-quality micro-habitats that were previously unoccupied (Miranda et al. 2000; Robb and Abrahams 2003). Interestingly, habitats that are high in complexity and lower in DO are typically low in predation-risk (Savino and Stein 1982; Burleson et al. 2001), thus survival might improve since sunfish can tolerate some risks associated with low DO (Miranda et al. 2000). In this study, we did not consider how spatial heterogeneity of prey availability within macrophyte beds might influence *Lepomis* spp. habitat selection (see Colon-Guad et al. 2004; Theel et al. 2008). Such bottom-up effects could influence optimal habitat selection of *Lepomis* spp. within dense macrophyte beds thereby modifying optimal management strategies of invasive macrophytes; this can be especially important given dynamic influences between DO and habitat complexity on *Lepomis* spp., their prey (e.g., macroinvertebrates), and their predators (e.g., largemouth bass). Overall, density-dependent processes indicated that sunfish utilization of hypoxia habitats reflected a high density population, and increasing utilization of those habitats may reflect positive population growth. If this is the case, monitoring programs might focus more intensely on quantifying temporal changes in fish occurrence within low-quality habitats to more clearly evaluate problematic areas associated with hydrilla.

Density-dependent habitat selection (DDHS) appeared to lead to inconsistent relationships between habitat quality and habitat use (Fretwell and Lucas 1970; Morris 1987). Ultimately, DDHS could influence the methods required for evaluating problematic areas associated with invasive macrophytes. Monitoring

programs often use initial assessments of animal densities across habitat gradients to calibrate management's definition of habitat quality assuming that animal density and habitat quality are correlated (Van Horne 1983; Fielding and Bell 1997). Without sufficient information on microhabitat utilization corresponded to in situ measures of microhabitat quality, there may be inadequate translation of animal-habitat relationships to the spatial-scales where management operates. Hence, fish-microhabitat relationships are needed to interpret the process of habitat selection and extrapolate to broader spatial scales (Van Horne 1983; Dibble et al. 1996). This study showed that, independently, neither fish occurrence nor count surveys indicated habitat quality across all population densities within hydrilla beds. Use of both count and occurrence data were needed to identify density-dependence in the sunfish-habitat quality relationship. Management must consider how sampling tactics used to monitor habitats has consequences for interpreting habitat selection. Resource managers can better evaluate both fish-macrophyte relationships and the potential consequences of density-dependence contrasting cost-effective occupancy surveys with growth, diet, and survival data from their fish species of interest. This alleviates managers from quantifying cost-prohibitive, data-intensive abundance patterns (e.g., mark-recapture methods) while still obtaining most of their data needs for understanding the drivers in fish population dynamics.

These results provide some of the first insights that fish microhabitat use within an invasive macrophyte is density-dependent and nonlinear. In addition, we highlighted the population-level consequences of this use, showing that sunfish populations can thrive in previously deemed inhospitable habitats. Sampling programs need to consider DDHS processes because commonly utilized fish surveying methods did not always appropriately track relationships between fish and habitat qualities across all fish densities. Restoration plans can address whether invasive macrophytes influence native fish habitats more effectively by contrasting fish counts and occurrence across habitat gradients. Such an evaluation can determine the appropriate control and restoration actions for invasive macrophytes.

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