ARTICLE

Drought-driven lake level decline: effects on coarse woody habitat and fishes

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Abstract: Research testing for the effects of climate change on lentic fishes has focused on changing thermal and dissolved oxygen regimes, but has often overlooked potential influences of altered lake levels on littoral habitat availability and species interactions. Natural littoral structures such as coarse woody habitat (CWH) can be critical to fishes for prey production, refuge, and spawning. Drought-driven lake level declines may strand these structures above the waterline and thereby remove them from littoral zones. A prolonged drought in northern Wisconsin, USA, allowed us to test for effects of lake level decline on CWH and the response of a fish community. During our study (2001–2009), the lake level of Little Rock Lake South declined over 1.1 m and >75% of the previously submerged CWH was lost from the littoral zone. The loss of CWH coincided with the forage fish species (yellow perch, *Perca flavescens*) falling below detection and reduced growth of the top piscivore (largemouth bass, *Micropterus salmoides*). Our study highlights the importance of lake level fluctuations as a mechanism by which climate change may affect aquatic ecosystems and species interactions.

Résumé : La recherche sur la détection des effets des changements climatiques sur les poissons lentiques s'est axée sur la modification des régimes thermique et d'oxygène dissout, sans trop s'attarder aux effets possibles de la modification des niveaux des lacs sur la disponibilité d'habitats littoraux et les interactions entre espèces. Des structures littorales naturelles comme les habitats constitués de débris ligneux grossiers (DLG) peuvent être essentielles aux poissons pour la production de proies et le frai, et comme refuges. La baisse du niveau d'un lac découlant de la sécheresse peut faire en sorte que ces structures se retrouvent au-dessus de la ligne des eaux et soient ainsi retranchées des zones littorales. Une sécheresse prolongée dans le nord du Wisconsin (États-Unis) nous a permis de vérifier les effets de la baisse du niveau des lacs sur les habitats de DLG et la réaction de la communauté de poissons. Durant l'étude (2001–2009), le niveau du lac Little Rock Lake South a baissé de 1,1 m, et >75 % des DLG auparavant submergés ont été retranchés de la zone littorale. Cette perte de DLG coïncide avec une diminution de l'abondance de l'espèce de poisson proie (perchaude, *Perca flavescens*) sous la limite de détection et une baisse de la croissance du piscivore supérieur (achigan à grande bouche, *Micropterus salmoides*). Notre étude souligne l'importance des fluctuations des niveaux des lacs comme mécanisme par lequel les changements climatiques peuvent influer sur les écosystèmes aquatiques et les interactions entre espèces. [Traduit par la Rédaction]

Introduction

Current and projected rates of climate change and its associated influences on ecosystems are unprecedented in human experience (Heino et al. 2009). Effects of climate change have been and remain major areas of concern for freshwater ecosystems and fisheries (Ficke et al. 2007; Carpenter et al. 2011). This is particularly true in the Laurentian Great Lakes region (Meisner et al. 1987; Lynch et al. 2010), where fisheries and other recreational activities are focused on lakes (Postel and Carpenter 1997; Wilson and Carpenter 1999) and are pillars of local and regional economies (Peterson et al. 2003). Shifts in thermal and dissolved oxygen regimes have been the principal focus of research on climate change effects on fishes (Magnuson et al. 1997; Heino et al. 2009; Lynch et al. 2010). While this research has shown that changes in thermal and dissolved oxygen regimes may reduce available habitat for many cold-water species, in many lakes cool- and warm-water species are likely to benefit (e.g., De Stasio et al. 1996; Magnuson et al. 1997; Heino et al. 2009). Nevertheless, understanding these potential climate effects is critical as changes in physical characteristics may alter species abundances (e.g., Casselman 2002), shift

species distributions and ranges (e.g., McLain et al. 1994; Sharma et al. 2007), and cause local extirpations (e.g., Lyons et al. 2010; Sharma et al. 2011). Fishes and fisheries may also be substantially affected by climate-driven changes in habitat and predator–prey interactions (Jones et al. 2006). We examine one such potential mechanism: the effects of drought-induced lake level reduction on littoral habitat, specifically coarse woody habitat (CWH).

Climate change may cause droughts (Lake 2011; Romm 2011) that could severely alter freshwater ecosystems (Carpenter et al. 2011; Ledger et al. 2011; Morrongiello et al. 2011a). Lake levels of small inland lakes may be particularly sensitive to climate change because of high surface area to volume ratios relative to large lakes (Schindler et al. 1990; Adrian et al. 2009). Lake level reductions of up to 1 m have been observed in such lakes in the Laurentian Great Lakes region during recent droughts (Magnuson et al. 1997; Nadelhoffer et al. 2009), a trend likely to continue with climate change (Mortsch and Quinn 1996; Schindler 2009). Reduced lake levels generally decrease littoral habitat (Ficke et al. 2007; Lake 2011), which is critical to aquatic food webs (Strayer and Findlay 2010). Fishes across all trophic levels are known to rely heavily on littoral food sources (Vadeboncoeur et al. 2002), with

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316

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

littoral zones supporting 65% of the consumption by lentic fish communities (Vander Zanden and Vadeboncoeur 2002) and 57% of their body carbon (Vander Zanden et al. 2011). The effects of lake level changes over a few days to months have been studied in reservoirs (e.g., Wilcox and Meeker 1992; Ozen and Noble 2002; Matthews and Marsh-Matthews 2003), and annual cycles of water level changes are known to be important for growth and production of river fishes (e.g., Junk et al. 1989; Gutreuter et al. 1999; Zeug and Winemiller 2007). However, the effects of multiyear lake level reductions on littoral habitat and lake food webs have received little attention in climate change fisheries research (Ficke et al. 2007; Lynch et al. 2010).

Littoral zone structures are important to fishes (Smokorowski and Pratt 2007), but may be lost as lake levels decline (Ficke et al. 2007). For instance, fallen trees (CWH) serve as refuge for fishes (Sass et al. 2006b; Roth et al. 2007) and their invertebrate prey (Vander Zanden and Vadeboncoeur 2002; Roth et al. 2007) as well as spawning habitat (Lane et al. 1996; Hunt and Annett 2002; Lawson et al. 2011). CWH has also been associated with forage fish survival (Sass et al. 2006a) and fish growth (Schindler et al. 2000; Sass et al. 2006b). However, CWH is generally stationary in the littoral zone, and reduced lake levels could leave CWH stranded along shorelines and unavailable to fishes and their prey. Natural accumulation of CWH into lake littoral zones is a slow process, and replacement of CWH can take centuries (Guyette and Cole 1999; Roth et al. 2007). Testing whether fish communities respond to the loss of littoral structures under reduced lake level conditions is critical for understanding the potential effects of climate change on lentic ecosystems.

In recent decades, Wisconsin's Northern Highland Lake District has endured several droughts (Webster et al. 1996; Kucharik et al. 2010; WICCI 2012) akin to those expected in many temperate regions under future climate change scenarios (Kling et al. 2003; Schindler 2009; Lynch et al. 2010). We used a seepage lake within this district as a model system to test for the effects of reduced lake level on CWH and the fish community. We tested for (*i*) a relationship between lake level and submerged CWH available to fishes and (*ii*) the response of fishes to sustained losses in available CWH. We hypothesized that lake level reductions as a consequence of drought would decrease the amount of littoral CWH available to fishes, have a negative effect on prey fish densities, and reduce piscivore growth rates.

Methods

Study species

The largemouth bass (*Micropterus salmoides*; hereafter bass) is a recreationally important freshwater fish species inhabiting lakes, impoundments, rivers, and streams throughout much of North America (Carlander 1977; Becker 1983). In 2006, *Micropterus* spp. were the most sought after group of fresh or saltwater fishes by recreational anglers (US Department of the Interior et al. 2008), and bass are commonly sought by Wisconsin anglers, who released 97% of captured individuals (Gaeta et al. 2013). Bass is often the apex predator in aquatic systems (Noble 2002) and sometimes acts as a keystone species (Mittelbach et al. 1995). Wisconsin is near the northern extent of this species distribution (Becker 1983). Although stunted populations are not uncommon, bass in northern latitudes generally mature at 3–4 years of age (254–305 mm) (Becker 1983). Bass can reach Wisconsin's minimum length limit for recreational harvest of 356 mm in as little as 4–5 years (Mraz and Threinen 1957) or as long as 12–15 years (Gaeta et al. 2011) and have a maximum length of about 500 mm (Becker 1983). Densities in the upper Midwest have been documented to range from 1 to 356 bass·ha^{-1} (Freedman et al. 2012).

Yellow perch (*Perca flavescens*; hereafter perch) is a common panfish (i.e., small sport fish targeted primarily for consumption) in Wisconsin and is often sought by anglers (Beard and Kampa 1999).

The upper length observed in Wisconsin waters is about 250 mm (Becker 1983). Perch serves as an important forage fish for many sport fishes, including bass.

Study site

Little Rock Lake is an 18 ha, oligotrophic, seepage lake with low macrophyte densities (Sass et al. 2006a) located in Wisconsin's Northern Highland Lake District (Vilas County; 45°59′46.49″N, 89°42′17.01″W). This district is one of the densest lake regions in the world with 13% of the landscape covered by lakes (Magnuson et al. 2006; Hanson et al. 2007; Buffam et al. 2011). Little Rock Lake was divided into two basins in the 1980s with a polyvinyl chloride curtain creating treatment (10 ha, 10.5 m maximum depth; hereafter Little Rock North) and reference (our study site; hereafter Little Rock South) basins. The area, perimeter, and maximum depth of Little Rock South (8.1 ha, 1.4 km, and 6.5 m, respectively; Gaeta et al. 2011) are all slightly greater than the regional median (5.4 ha, 1.1 km, and 4.0 m, respectively; Hanson et al. 2007). Little Rock North and South contain fish communities historically dominated by bass and perch. Black crappie (*Pomoxis nigromaculatus*), rock bass (*Ambloplites rupestris*), and central mudminnow (*Umbra limi*) are also present at low abundances.

Little Rock North was the site of an experimental whole-lake reduction of CWH (July–August 2002), while CWH in Little Rock South was left undisturbed as a reference system. Details of the manipulation and responses of the fish community to this CWH reduction from 2001 to 2004 can be found in Sass et al. (2006b). Shortly after the initial CWH study, a drought reduced lake levels in seepage lakes across the region, including both basins of Little Rock Lake. Natural lake level reductions left formerly submerged CWH stranded along the shoreline of Little Rock South (Fig. 1). To test for fish community responses to this natural reduction of CWH, monitoring continued during May–September 2005 and 2007–2009. As a part of another experiment in Little Rock North, we also stocked 384 adult bass from Little Rock North into Little Rock South in late July – early September 2007. The stocking provided a broader range of bass densities, which may have increased the power of our analysis to detect density effects.

Quantifying lake level

Little Rock Lake levels were not directly measured during our study. To estimate lake level over time, we fitted a linear model to compute Little Rock Lake levels from levels of nearby Big Muskellunge Lake (Appendix A). The model was calibrated using data from 1984 to 1996, when levels of both lakes were monitored; Little Rock Lake was monitored by the United States Geological Survey (USGS) (Rose 1993) and Big Muskellunge Lake by the North Temperate Lakes Long Term Ecological Research (NTL-LTER) Program (Stanley 2012). Model projections of lake level (1996–2010) showed that Little Rock Lake underwent a maximum lake level loss of >1.1 m during the study period (June 2001 – August 2009; maximum level = 495.74 m above sea level, minimum level = 494.63 m above sea level; Fig. 2a).

Quantifying CWH

To quantify the relationship between lake level and CWH, we surveyed CWH along eight transects moving clockwise from cardinal and intercardinal directions relative to the center of the lake basin during July 2009. Transects were 50 m long, as measured along the high-water mark, which we identified by the presence of leatherleaf (*Chamaedaphne calyculata*). Our survey covered 28.6% of the lake perimeter. Every piece of CWH along the transect from the high-water mark to the 2.5 m depth contour (i.e., 2.5 m below the high-water mark) was measured. Woody structures were classified as CWH if the logs were ≥1.5 m long, ≥5 cm in diameter at the widest point (Stanley 2002), and had less than half of their diameter buried in the sediment. We used these data to estimate the amount of CWH per kilometre of shoreline in the littoral zone of Little Rock

Fig. 1. Coarse woody habitat left stranded on the shoreline of Little Rock Lake South, Wisconsin, on 13 October 2007 (0.87 m lake level loss; 54.7% coarse woody habitat density reduction). Photo credit: J. Gaeta.

South at millimetre increments of lake level from the high-water mark to 2.5 m below the high-water mark (Appendix A). To generate a time series of CWH values, the estimates of the amount of CWH at lake level were applied to the projected time series of Little Rock South lake levels.

From 2001 to 2009, CWH spanned nearly the entire possible range of densities (Fig. A2). Only 7% of the available CWH was lost from 2001 to 2004 because of minor lake level fluctuations (Fig. 2b). Over the entire study period (2001–2009), about 76% of the CWH was naturally stranded from the littoral zone by lake level decline, a change from 662.5 to 160 logs·km⁻¹.

Fish sampling and analyses

Fish sampling methods are detailed in Sass et al. (2006b) and briefly described here. The fish community was sampled during May–September at fortnightly to monthly intervals from 2000 to 2005 and 2007 to 2009. Juvenile perch were sampled using unbaited minnow traps in 2003–2005 and 2007–2009; catch per unit effort (CPUE) was calculated as fish·trap⁻¹·day⁻¹. Minnow traps were deployed during 24 h trapping events. The traps were placed at a depth of about 0.25–1.5 m and we attempted to space them evenly along the shoreline. In 2003, we deployed 10 minnow traps per event. The mean number of minnow traps deployed per event in 2004, 2005, 2007, 2008, and 2009 were 20, 20, 25, 19.7, and 20 minnow traps, respectively. Bass were collected via angling because lake conductivity was too low for effective electrofishing. All bass ≥150 mm were marked with individually numbered Floy tags. We used the Chapman-modified, continuous Schnabel mark–recapture method to calculate annual population density estimates (fish·ha⁻¹) with 95% confidence intervals for bass ≥150 mm (Ricker 1975). Changes in lake area associated with lake level reductions were accounted for using the lake basin area to lake level relationship developed by Rose (1993) for Little Rock South.

Bass scales were used to determine size-specific growth rates. Scales were used because the long-term nature of the study precluded harvesting individuals for otoliths. Age estimates from scales of older individuals can be particularly challenging (Maraldo and MacCrimmon 1979; Buckmeier and Howells 2003), but largemouth bass age estimates from scales are similar to those from otoliths up to age 13 (Maceina and Sammons 2006). The oldest aged individuals in our study were 10 years old (third quartile age = 7 years old), which is within the appropriate range in which scales can accurately age largemouth bass. Bass scales were collected from the region posterior to a depressed pectoral fin from 2007 to 2009. We aimed to collect scales from five individuals for every available 10 mm length increment (i.e., 150–160 mm, 160–170 mm, etc.) per year. Scales were sonicated, pressed between two glass slides, and read using a digital imaging system. Annual growth rates (mm·year⁻¹) were determined using the Fraser-Lee method of back-calculation with Carlander's correction constant of 20 mm for bass (Carlander 1982).

All statistical tests were performed in R Cran statistical package (version 3.0.1; R Development Core Team 2013). We tested whether perch CPUE changed over time by performing a nonparametric multiple comparison test of perch CPUE among years following a Kruskal–Wallis test (R Cran package "pgirmess" version 1.5.4) (Siegel and Castellan 1988). We quantified the relationship between CWH and the probability (Pr) of detecting perch using the following logistic model with trapping events nested within each year (Gelman and Hill 2008) via R Cran package lme4 version 0.999999-2:

(1)
$$\Pr(y_j = 1) = \text{logit}^{-1}(\alpha + \beta_1 \text{cwh}_j + a_j)$$
$$a_j \sim N(0, \sigma^2)$$

Fig. 2. Little Rock Lake South, Wisconsin, time series of predicted (*a*) lake level (m above sea level) and (*b*) coarse woody habitat density (no.·km⁻¹) throughout both study periods (gray boxes). Predictions of lake level were estimated using a linear model that computed Little Rock Lake levels from lake levels of nearby Big Muskellunge Lake (Appendix A). Coarse woody habitat density at lake level was surveyed; these measurements were applied to the time series predictions of lake level to estimate coarse woody habitat over time (Appendix A).
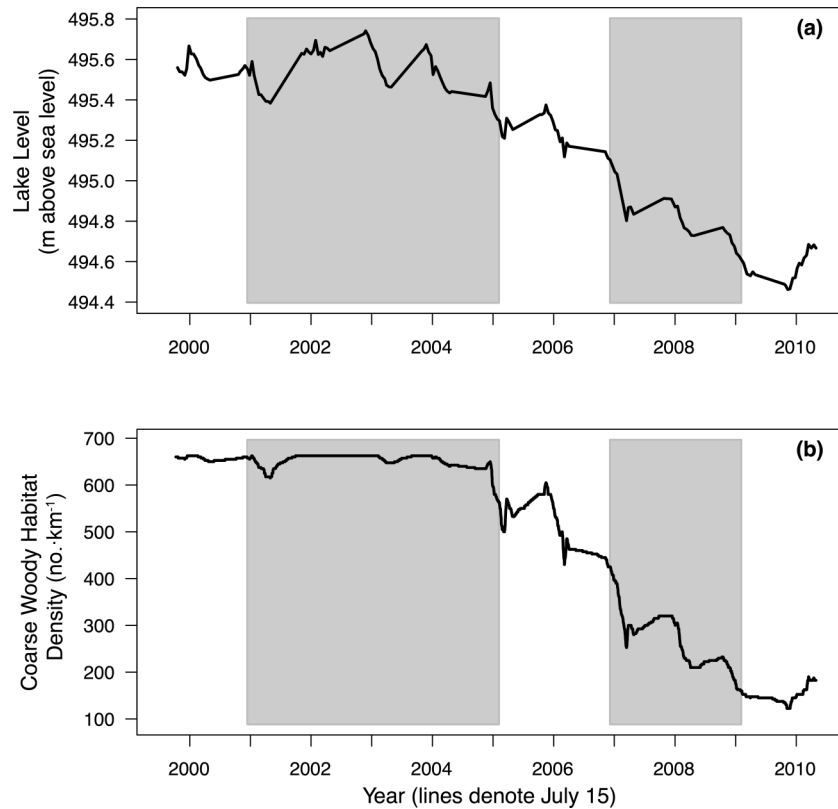
where y_j is the probability of detecting perch in year j, α is the model intercept, β_1 is the estimated effect of CWH density (no.·km⁻¹) on the probability of detecting perch, cwh_j is the CWH density during year j, and a_j is the random effect of year with a variance of σ^2. The model was compared with an intercept-only model to assess explained variance associated with the addition of CWH.

Our analysis of bass growth was composed of three steps. We first performed a forward step-wise selection procedure to identify the covariates associated with bass size-specific growth rate (mm·year⁻¹). We then took the derivative of the model with respect to CWH to determine the effect of CWH on size-specific growth. Finally, we used our growth model to simulate size-specific growth rates and growth trajectories for bass under high and low CWH conditions.

The bass growth data were hierarchically structured with annuli-specific growth observation (mm·year⁻¹) nested as repeated measures within individual fish and annuli observations among fish nested within various years. We obtained growth estimates from 433 annuli from 126 individual fish during seven years (2001–2005, 2007, and 2008). We used the following longitudinal multilevel modeling approach that accounted for repeated measures of annuli, as well as fish and year groupings, while identifying any relationship between log$_e$(growth) and the observed changes in fish length, CWH density, and bass density, which varied among study years:

$$
(2) \quad \begin{aligned} y_{ikj} &= \alpha + \boldsymbol{\beta}X_j + a_k + b_j + \varepsilon_{ikj} \\ a_k &\sim N\left(0, \sigma_a^2\right), \quad b_j \sim N\left(0, \sigma_b^2\right), \quad \varepsilon_{ikj} \sim N\left(0, \sigma_\varepsilon^2\right) \end{aligned}
$$

In eq. 2, y_{ikj} is the ith growth observation of the kth fish in the jth year, α is the mean of growth observations over all fish, $\boldsymbol{\beta}$ is a vector of coefficients of covariates X in year j, a_k and b_j are the random effects of individual fish and year with variances σ_a^2 and σ_b^2, respectively, and ε is the residual error term with variance σ_ε^2. Analyses followed Gelman and Hill (2008) as applied to fish growth in Gaeta et al. (2011) and Morrongiello et al. (2011b) using R Cran package "lme4" version 0.999999-2. Annuli from 2001 to 2005 and 2007 to 2008 were available for Little Rock South fish, and annuli from 2007 to 2008 were available for fish that were experimentally stocked from Little Rock North to Little Rock South in 2007. All covariates were grand-mean-centered prior to analysis to simplify the interpretation of the model results (Gelman and Hill 2008). Models were fit by maximum likelihood.

The evaluation of covariates in eq. 2 was based on a forward model selection procedure. We allowed the inclusion of the main effects log$_e$(length), length², CWH density, and bass density. We allowed for interactions among covariates when more than one main effect was included in the model (Agresti and Finlay 2009). However, we did not allow for interactions among length covariates to prevent collinearity. At each step, the addition of a covariate or interaction to the model was contingent upon a deviance information criterion (DIC) improvement of ≥7 (Burnham and Anderson 1998; Spiegelhalter et al. 2002). We allowed log$_e$(length) and length² to be included jointly in the model to account for logarithmic and quadratic relationships, respectively, between growth and length. That is, these covariates would account for a decline in growth that increases with length and a parabolic-shaped growth pattern with some optimal growth at intermediate lengths (e.g., 100–150 mm), respectively. The final model was fitted

Fig. 3. (*a*) Yellow perch (*Perca flavescens*) minnow trap catch per unit effort (CPUE; fish·trap⁻¹·day⁻¹) over time in Little Rock Lake South, Wisconsin, and (*b*) the probability (Pr) of detecting yellow perch in a 24 h minnow-trapping event along a gradient of coarse woody habitat (CWH) density (no.·km⁻¹) and percent reduction of CWH. In 2003, we deployed 10 minnow traps per event. The mean number of minnow traps deployed per event in 2004, 2005, 2007, 2008, and 2009 were 20, 20, 25, 19.7, and 20 minnow traps, respectively. CPUEs among years with matching letters were not significantly different (*p* > 0.05). The number of trapping events for each year is shown below boxplots. Boxplots are shown with medians, first and third quantiles, and the range. The gray circles (jittered) represent sample events in which yellow perch were detected or not (1, 0) at a given CWH density. The line represents the logistic model fit to minnow trap observations nested within year. The gray polygon illustrates the range of variance associated with the random effect of year (a_j).
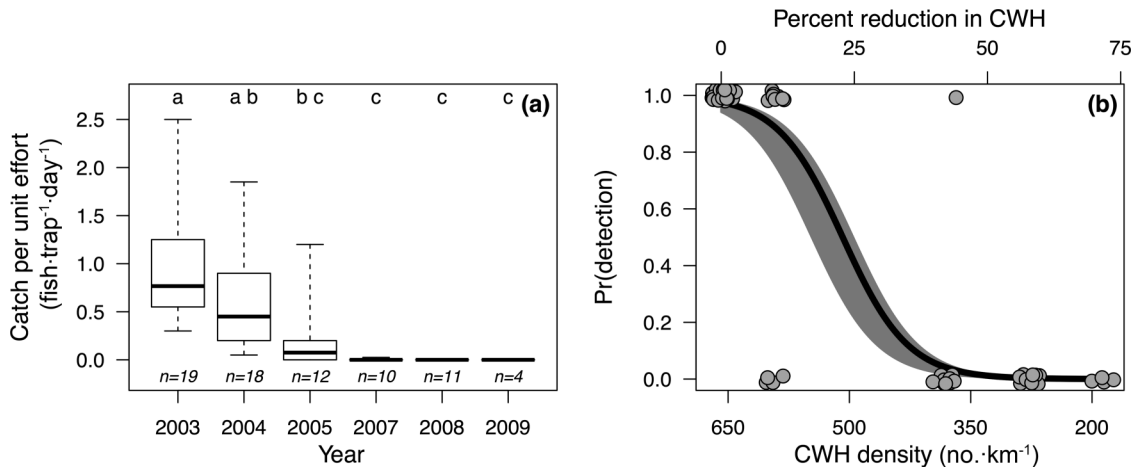

Table 1. Logistic regression analysis results of the probability of detecting yellow perch (*Perca flavescens*) as a function of coarse woody habitat (cwh) density (no.·km⁻¹) with 24 h trapping events (*n* = 74) nested within year (*j*; *n* = 6).

	Group	Parameter	Intercept model variance	Full model variance
Random effects	Year (intercept)	$\hat{a}_j$	3.28e+01	8.02e−01
	Parameter	Coefficient	Coefficient estimate	Standard error
Fixed effects	Intercept	$\hat{\alpha}$	−1.26e+01	3.95e+00
	cwh$_j$	$\hat{\beta}_1$	2.47e−02	6.91e−03

Note: In 2007, we deployed 10 minnow traps per event. The mean number of minnow traps deployed per event in 2004, 2005, 2007, 2008, and 2009 were 20, 20, 25, 19.7, and 20 minnow traps, respectively. Model structure is shown in eq. 1.

and compared with the intercept-only model. Residual diagnostics revealed no unexpected patterns (Smith and Draper 1998).

The relationship between CWH and fish growth was calculated as the derivative of eq. 2 with respect to CWH (hereafter the CWH density effect). The covariance matrix of model parameters was used to calculate the standard deviation of the CWH density effect via the standard error propagation formulae (Meyer 1975; Gaeta et al. 2011). The units of the CWH density effect are (mm·year⁻¹)/ (CWH·km⁻¹) and can be interpreted as the change in size-specific growth rate with the addition of one piece of CWH per kilometre of shoreline.

The complex relationships among predictors of bass growth motivated several growth simulations to parse out the relationship of size-specific growth rate with CWH. We simulated two scenarios of size-specific growth rate, modeling growth under the greatest and lowest annual densities of CWH observed during the growth portion of the study (i.e., 2001–2005, 2007, and 2008; 660 and 276 logs·km⁻¹, respectively). To understand how these different size-specific growth rates influenced bass length at age, we used the scenario simulated size-specific growth rates to then simulate bass growth trajectories. For each scenario, we initiated the model at the grand mean length at age 1 (81.7 mm).

Results

Perch CPUE declined over time, coinciding with the decline of CWH from the littoral zone due to reduced lake level (Fig. 3*a*). The disappearance of perch occurred over three years with the first

Fig. 4. Largemouth bass (*Micropterus salmoides*) density estimates (±95% confidence intervals) over time in Little Rock Lake South, Wisconsin, from 2001 to 2009. Post-stocking manipulation 2007 density is represented by the solid triangle.
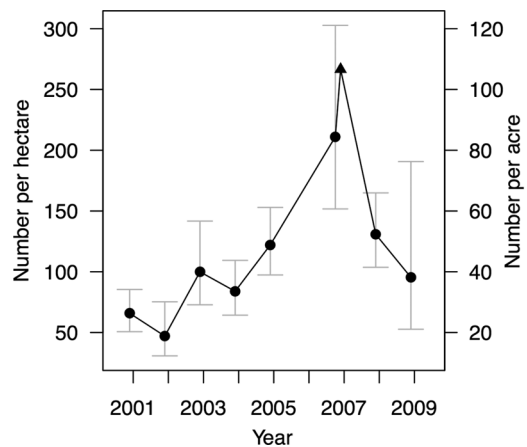
empty trap observed in 2005 and the last perch observed in 2007. No perch were detected in 2008 or 2009. The logistic regression model indicated that the probability of detecting a perch was <50% at 508 logs·km⁻¹ or a 23% reduction in CWH, <10% at 419 logs·km⁻¹ or a 36% reduction in CWH, and <1% at 322 logs·km⁻¹
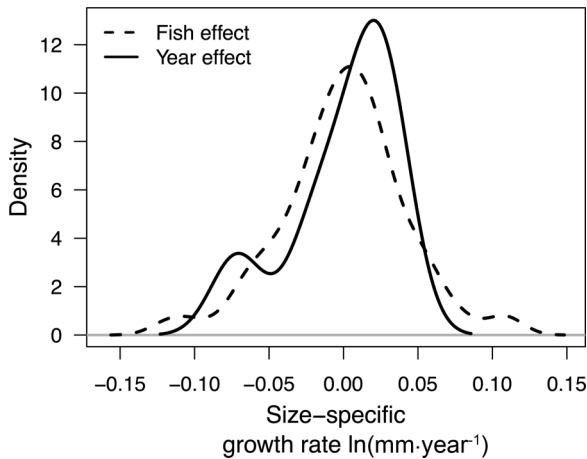
Table 2. Longitudinal multilevel linear regression analysis results of largemouth bass (*Micropterus salmoides*) size-specific growth rate (log$_e$-transformed) from Little Rock Lake South, Wisconsin, in 2001–2005, 2007, and 2008.

	Group	Parameter	Sample size	Intercept model variance	Selected model variance
Random effects	Fish (intercept)	$\hat{a}_k$	126	3.45e−01	9.54e−03
	Year (intercept)	$\hat{b}_j$	7	8.18e−01	2.43e−03
	Residual	$\hat{\varepsilon}_{ikj}$	433	1.33e−01	1.40e−01

	Parameter	Coefficient	Selected model coefficient estimate	Selected model standard error	Grand mean
Fixed effects	Intercept	$\hat{\alpha}$	3.89e+00	3.07e−02	
	$\log_e(l_j)$	$\hat{\beta}_1$	5.19e−01	1.01e−01	5.24
	l_j^2	$\hat{\beta}_2$	−2.19e−05	1.47e−06	50551.52
	cwh_j	$\hat{\beta}_3$	1.55e−03	2.21e−04	552.84
	$l_j^2 \cdot cwh_j$	$\hat{\beta}_4$	4.43e−08	5.86e−09	

Note: "*l*" represents length and "*cwh*" represents coarse woody habitat density. The variances of the random effects for both the intercept-only model and the selected model are shown. The grand mean is the value on which the parameters were centered. Model structure is shown in eqs. 2 and 3.

Fig. 5. Density estimates of random effects (best linear unbiased predictors) for the fish (a_k; dashed line) and year (b_j; solid line) levels of a longitudinal multilevel model fit as a function of size-specific growth rate (log$_e$-transformed) from Little Rock Lake South, Wisconsin, in 2001–2005, 2007, and 2008 as described in eq. 2.

Fig. 6. The effect of coarse woody habitat (CWH) density (±1 standard deviation; dashed lines) on size-specific largemouth bass (*Micropterus salmoides*) growth rate as a function of largemouth bass length in Little Rock Lake South, Wisconsin. A value greater than zero (gray line) indicates a positive relationship between CWH and growth rate; a value below zero indicates a negative relationship. Standard deviations were calculated from the covariance matrix of model parameters using standard error propagation formulae. Values of the CWH density effect can be interpreted as the effect on size-specific growth of adding one piece of CWH per kilometre of shoreline. Units are (mm·year^{-1})/(CWH·km^{-1}).
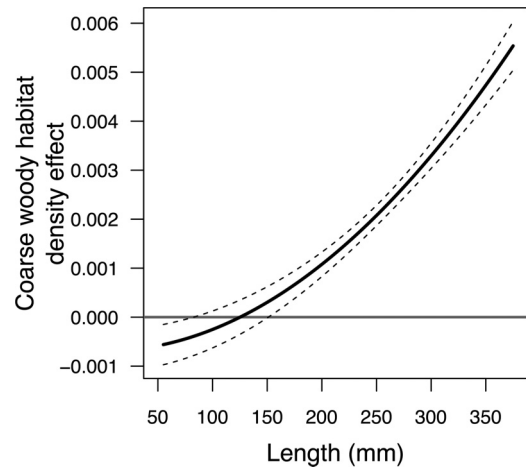

or a 50% reduction in CWH (Fig. 3b; Table 1). The inclusion of CWH significantly improved the model fit (intercept-only model DIC = 40.1, CWH model DIC = 27.5), accounting for 97.6% of the year variance.

Bass density varied during the study from 47 to 211 bass·ha^{-1} (Fig. 4). The stocking manipulation resulted in a 26% increase in bass density in Little Rock South. In general, bass density increased after habitat loss followed by a density reduction. Density tripled prior to the bass density manipulation in 2007 and subsequently returned to near initial levels by 2009.

Annuli observations ($n = 433$) were used to calibrate the growth model. Annuli observations per year (2001–2005, 2007, and 2008) ranged from 23 to 97 from fish ranging in age from 2 to 10 years old (mean of 4.2 years). Total lengths of bass sampled for scales ranged from 194 to 384 mm. Back calculated lengths at age ranged from 55.0 to 377.6 mm and size-specific growth rates ranged from 4.1 to 132.7 mm·year^{-1}. These annuli observations were used to fit eq. 2. The model selection process using eq. 2 resulted in the following fitted model:

$$(3) \quad y_{ikj} = \alpha + \beta_1[\log_e(l_j)] - \beta_2(l_j^2) + \beta_3(cwh_j) + \beta_4(l_j^2 \cdot cwh_j) + a_k + b_j + \varepsilon_{ikj}$$

where y_{ikj} is the ith growth observation (log$_e$-transformed) of the kth fish in the jth year, and l and cwh are the individual bass length and CWH density for each year j, respectively. The fitted parameters are presented in Table 2. The best linear unbiased predictors for both the fish (a_k) and year (b_j) were plotted using a density function in R Cran using a Gaussian kernel and the default smoothing bandwidth (Fig. 5). Relative to the intercept-only model, the DIC was reduced by a value of 255.3. Model residuals showed no trends when plotted against covariates.

Bass growth rate was positively correlated with CWH (Table 2); however, the relationship between growth and CWH varied across fish length. The derivative of the model with respect to CWH was calculated to illustrate how CWH was related to growth across fish length (Fig. 6). CWH was negatively correlated with growth of small bass (<80 mm) and positively correlated with growth of most mass lengths (i.e., individuals >152 mm). The strength of the positive relationship between bass length and CWH density increased with fish length.

Fig. 7. Simulated largemouth bass (*Micropterus salmoides*) (*a*) size-specific growth rates as a function of largemouth bass length and (*b*) growth trajectories under the range of coarse woody habitat (CWH) observed from 2001 to 2005, 2007, and 2008 in Little Rock Lake South, Wisconsin. The horizontal gray, dotted line represents the minimum legal length limit in the region of 356 mm. The greatest and lowest observed annual densities of CWH were 660 and 276 logs·km^{-1}, respectively.
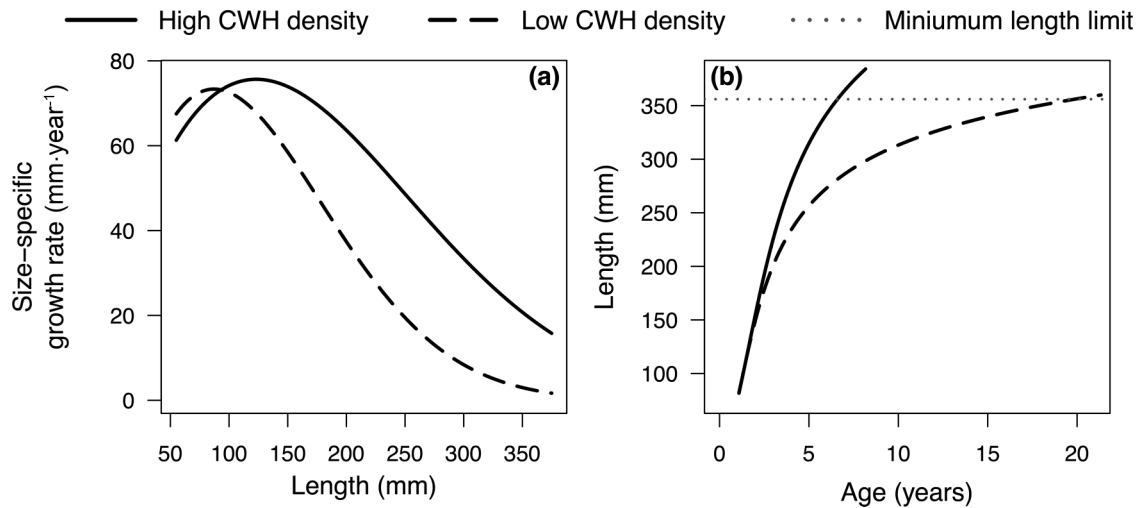
Growth rate simulations identified a difference in growth patterns between bass in the high and low CWH scenarios. The maximum size-specific growth rate for the low CWH bass occurred at about 88 mm and rapidly declined with length to a growth rate of <2 mm·year^{-1} above 370 mm (Fig. 7*a*). Conversely, the maximum size-specific growth rate for the high CWH bass occurred at about 124 mm and more gradually declined with length. In the high CWH scenario, bass maintained a growth rate of >15 mm·year^{-1} through all simulated lengths. Simulations of growth trajectories indicated that bass reach Wisconsin's minimum length limit of 356 mm in about 6.5 years under high CWH conditions, but take nearly 20 years under low CWH conditions (Fig. 7*b*).

Discussion

A multiyear drought in Wisconsin's Northern Highland Lake District offered a unique opportunity to test for the effects of climate-induced habitat loss on structural littoral refuge in the form of CWH and a fish community. After a lake level decline of >1.1 m, about 76% of formerly submerged littoral CWH became inaccessible to fishes. The loss of CWH was associated with the forage fish species (perch) falling below detection and the decline of apex predator (bass) growth rates.

The rapid decline of the perch population was associated with the loss of available CWH. Perch first failed to appear in a trapping event in 2005, after only a 10% loss of CWH. No perch were detected in 2008 or 2009 after 58% and 72% of the available CWH had been stranded from the littoral zone, respectively. The mechanism driving the decline in perch cannot be inferred from our study. However, several unmeasured biotic or abiotic factors such as altered thermal or dissolved oxygen regimes, reduced prey resources, altered sampling efficiency, loss of spawning habitat, and (or) increased predator–prey encounter rates could have contributed to the observed reduction in the perch population. Previous research has suggested the potential for predator–prey encounter rates to increase with reduced CWH (Sass et al. 2006*a*), which would result in intense bass predation on perch as CWH declined. Bass is a generalist that forages optimally (Hodgson and Kitchell 1987), making perch a favored prey item in Little Rock South (Sass et al. 2006*b*). Furthermore, Sass et al. (2006*a*) found that perch predation risk was lower in CWH than at the edge of CWH or away from refuge, precisely where reduced lake level forced perch to reside. Given this potential mechanism, the severe depletion of the perch population might have been exacerbated

by the relatively high densities of bass in Little Rock South (Freedman et al. 2012), which initially increased with reduced lake level. Conversely, this depletion might have been dampened by a more complex food web offering alternative high-energy prey to bass. The strength of this relationship may also be weakened in lakes with alternative littoral habitat such as boulders, cobble, or macrophytes (Savino and Stein 1989; Sass et al. 2006*a*).

Our growth analysis indicated that size-specific growth rate of bass was related to length and CWH density. In general, growth declined with length, following a logarithmic growth trajectory (Isely and Grabowski 2007). The relationship between length and growth was complex, perhaps because of changing growth responses as yearling bass shifted from invertebrate to fish prey (Olson 1996). Growth was positively correlated with CWH, indicating that the loss of CWH was associated with decreased growth rates. However, the inclusion of the interaction between CWH and length^2 indicated that this relationship was complex and the strength of this relationship varied across length.

The observed changes associated with lake level and CWH loss have implications for fisheries, as bass simulated under low CWH conditions took nearly 20 years to reach the minimum legal length limit. Bass density was not included in the model, suggesting that a management strategy that reduced bass density, via increased harvest for instance, may not offset the negative growth effects of reduced CWH. However, bass densities in our study ranged from 47 to 211 bass·ha^{-1}, a greater reduction in bass densities may compensate for the reduction in CWH.

Slow growing populations of bass in lakes with low CWH densities have previously been documented in Wisconsin (Schindler et al. 2000; Gaeta et al. 2011). In a cross-lakes survey of 16 lakes, Gaeta et al. (2011) found that bass take nearly 15 years to reach the Wisconsin legal length minimum in lakes with less than 125 logs·km^{-1}. Another plausible mechanism for the observed changes in bass growth and the fish community that deserves further research is the potential increase in predator–prey encounter rates and a subsequent depletion in available prey sources as the loss of CWH altered the foraging arena (Walters and Juanes 1993; Walters and Martell 2004).

Although few empirical studies have tested for the effects of climate-driven drought on fish populations (Ficke et al. 2007), Morrongiello et al. (2011*b*) tested similar questions in two Australian impoundments. They tested for a relationship between lake level and growth of a generalist piscivore, golden perch (*Macquaria*

322

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

ambigua), and similarly found that growth decreased with lake level. The authors hypothesized that habitat loss associated with lake level declines could drive this trend. Our study supports their hypothesis, associating lake level with littoral habitat and the availability of energetically profitable prey. The similarity of our findings is noteworthy given the divergent characteristics of our study systems. Little Rock South is a small, glacial, north-temperate lake in a lake-rich landscape while the study systems of Morrongiello et al. (2011*b*) were two large, man-made impoundments with surface inflows and outflows in an arid Australian climate. Despite these differences, our findings draw the same conclusion; climatic-driven lake level loss is associated with slower growing piscivores.

Our study documents the response of a fish community to lake level reductions. While the response of lakes to drought conditions may vary with landscape position (Webster et al. 1996), the majority of lakes in Wisconsin are seepage lakes (i.e., negative lake order and high landscape position; Riera et al. 2000), comprising >71% of Wisconsin lakes >1 ha (A.W. Latzka, University of Wisconsin – Madison, unpublished data, 2013). Likewise, the influence of climate change may also vary geographically, resulting not only in directional changes in lake level, but also increased lake level fluctuations (Adrian et al. 2009). Nevertheless, recent research has shown that the population-level effects of CWH loss may not be reversible on short times scales (i.e., <5 years). Sass et al. (2012) found that the addition of CWH was associated with changes in fish behavior (i.e., habitat use and foraging behavior), but did not result in altered population dynamics (i.e., growth rates, densities, or size structure) for the fish community. These findings suggest that low lake level periods during lake level fluctuations may have long lasting consequences.

Drought effects may foreshadow future responses of lakes to climate change (Morrongiello et al. 2011*a*; Hardie 2013), yet drought-driven lake level reduction has only recently gained attention as a critical lake response to global change (Ficke et al. 2007; Lake 2011; Morrongiello et al. 2011*b*). For instance, recent work by Hardie (2013) revealed that drought-driven reductions in lake level were associated with degraded spawning habitat and reduced larval fish densities. The drought we observed in northern Wisconsin allowed us to evaluate another potential mechanism, a quantitative link from climate to structural habitat and fish population dynamics — a link that is largely missing from existing predictive models of climate change effects on fishes (Jones et al. 2006).

Our research and the findings of both Morrongiello et al. (2011*b*) and Hardie (2013) emphasize the need to consider alternative or novel management practices as landscapes are altered by climate change. Management strategies that maintain littoral structures could mitigate the effects we observed. For instance, the addition of trees or other structures to deeper waters and along steep shorelines may offset some of the adverse effects of lake level reduction. Our research highlights the need to consider preventative management strategies to increase the resiliency of aquatic ecosystems to climate change.

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Appendix A. Quantifying lake level and CWH densities over time

Methods

Quantifying lake level

Little Rock Lake levels were not directly measured during our study. To estimate lake level over time, we fitted a linear model to compute Little Rock Lake levels from levels of nearby Big Muskellunge Lake. The model was calibrated using data from 1984 to 1996 when levels of both lakes were monitored; Little Rock Lake daily stage was monitored by the USGS (Rose 1993) and Big Muskellunge Lake stage was monitored fortnightly during the ice-free season by the NTL-LTER Program (Stanley 2012). The data were centered by subtracting the grand mean and converted into a rate:

$$(A.1) \qquad \left[\frac{cLRL_{t+1} - cLRL_t}{(t+1)-t}\right] = f\left[\frac{cBML_{t+1} - cBML_t}{(t+1)-t}\right]$$

where t and $t + 1$ are the current and next time step, respectively, and $cLRL_t$, $cLRL_{t+1}$, $cBML_t$, and $cBML_{t+1}$ are the centered Little Rock Lake level at the current and subsequent time steps and centered Big Muskellunge Lake level at the current and subsequent time steps, respectively. By analyzing the first difference of the lake level (level at time $t + 1$ minus level at time t) we eliminated autocorrelation in the time series, which could bias parameter estimates (Box and Jenkins 1976).

After the model was fit, we used Big Muskellunge Lake level observations to project Little Rock Lake levels from the last USGS observation in October 1996 through the duration of our study. Unfortunately, the lake levels observed during the course of our study were lower than those observed from 1984 to 1996, resulting in extrapolation beyond the observed levels to model projected lake levels from 1996 to 2010. We calculated 95% confidence intervals around our lake level projections by bootstrapping via resampling residuals. We ran 10 000 bootstrap iterations, extracted the model coefficients, and calculated 95% confidence intervals of the model coefficients.

Quantifying CWH

To quantify the relationship between lake level and CWH, we surveyed CWH along eight transects moving clockwise from cardinal and intercardinal directions relative to the center of the lake basin during July 2009. Transects were 50 m long, as measured along the high-water mark, which we identified by the presence of leatherleaf. The survey covered 28.6% of the lake perimeter. Every piece of CWH along the transect from the high-water mark to the 2.5 m depth contour (i.e., 2.5 m below the high-water mark) was measured. Woody structures were classified as CWH if the logs were ≥1.5 m long, ≥5 cm in diameter at the widest point (Stanley 2002), and had less than half of their diameter buried in the sediment. Any piece of CWH partially within the lateral and 2.5 m depth bounds of the transect was counted if the portion within the transect met the classification of CWH. Only portions of logs within the lateral transect boundary were measured. However, if ≥1.5 m of the CWH was within 2.5 m of the high-water mark, the surface length and maximum depth of the log within the lateral transect boundary was measured. The maximum height and depth, relative to the current lake level, and the surface length (length of CWH parallel to lake surface) were measured on each piece of CWH.

We estimated the amount of CWH·km⁻¹ in the littoral zone of Little Rock South at millimetre increments of lake level from the high-water mark to 2.5 m below the high-water mark. For each log at a given level, the submerged length of the log was calculated using triangle similarity ratios and the Pythagorean theorem. The surface length and maximum depth of each log were treated as the sides of a right triangle with the submerged length of the log as the hypotenuse. After the length of a log was estimated at a given lake level, we determined whether the log met the CWH criteria. If the criteria were met, the log was counted as CWH. Otherwise, the log was not considered active CWH in the lake at that particular lake level. This was repeated for each log at millimetre increments of lake level from the high-water mark to 2.5 m below the high-water mark. This procedure assumes logs are straight and may underestimate the actual length of a log. To generate a time series of CWH values, the estimates of the amount of CWH at lake level were applied to the projected time series of Little Rock South lake levels.

Results

Lake level

Little Rock Lake level was predicted using Big Muskellunge Lake level observations (Fig. A1a) with the following rate model (R^2 = 0.57, df = 162, $p < 0.001$):

$$(A.2) \qquad \left[\frac{cLRL_{t+1} - cLRL_t}{(t+1)-t}\right] = \alpha + \beta_1\left[\frac{cBML_{t+1} - cBML_t}{(t+1)-t}\right] + \varepsilon$$

where the intercept α was –6.04e–05 (SE = 1.17e–04), the rate coefficient β_1 was 0.77 (SE = 5.22e–02), and the model residual ε had a SE of 1.47e–03. Model residuals of the rate model were not autocorrelated. Model predictions of lake level corresponded closely with observations (R^2 = 0.99; Fig. A1b). Model projections of lake level (1996–2010) showed that Little Rock Lake underwent a maximum lake level loss of >1.11 m during the study period (June 2001 – August 2009; maximum level = 495.74 m above sea level, minimum level = 494.63 m above sea level; Fig. A1c). Bootstrapped 95% confidence intervals indicated that error associated with the model projections was negligible, with the maximum 95% confidence intervals of lake level error during the study period being ±0.01 m, which is less than 1% percent of the total observed lake level fluctuation.

CWH density

CWH density showed a sigmoidal relationship with lake level (Fig. A2). The upper asymptote was located at the maximum

Fig. A1. (*a*) Lake level observations from Little Rock Lake (black) and Big Muskellunge Lake (gray) (Wisconsin) from 1984 to 1996, (*b*) Little Rock Lake level model predictions plotted against observations from 1984 to 1996 ($R^2 = 0.99$), and (*c*) Little Rock Lake level projections (black) estimated from Big Muskellunge Lake level observations (gray). Estimates were computed using an autocorrelation correction linear rate model (eq. A.1, $R^2 = 0.57$, df = 162, $p < 0.001$) of Little Rock Lake United State Geological Survey observations (1984–1996) as a function of nearby Big Muskellunge Lake North Temperate Lakes Long Term Ecological Research observations (1984–2010). Study periods (gray boxes are shown. Primary and secondary *y*-axis scales are consistent across panels.
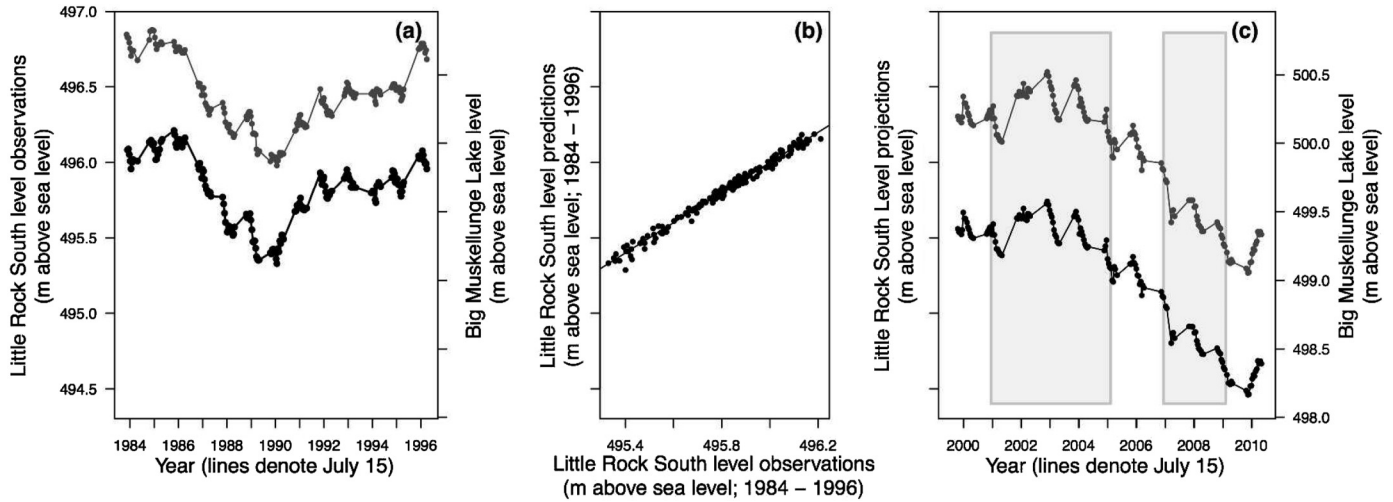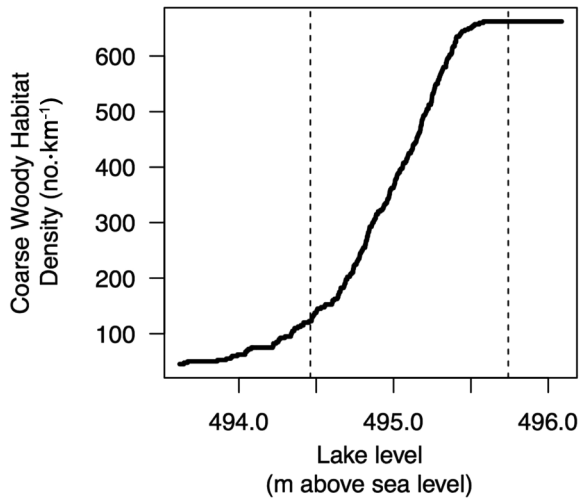

Fig. A2. Estimates of the Little Rock Lake South, Wisconsin, coarse woody habitat density (no.·km⁻¹) at lake level (m above sea level) from the high-water mark to the 2.5 m depth contour. Estimates were calculated in 1 mm increments. The range of lake levels observed during the 2001–2009 study period (vertical dashed lines) are shown.

amount of CWH available in the system and the lower asymptote near zero (i.e., all CWH eliminated from the littoral zone). From 2001 to 2009, CWH spanned nearly the entire possible range of densities (Fig. A2). Only 7% of the available CWH was lost from 2001 to 2004 because of minor lake level fluctuations (Fig. A2). Over the entire study period (2001–2009), 75.8% of the CWH density was naturally removed from the littoral zone by lake level decline, a change from 662.5 to only 160 logs·km⁻¹. Error (95% confidence intervals) around the CWH estimate due to the uncertainty around our lake level estimates (maximum of ±0.01 m of lake level) was negligible. The maximum error associated with the 95% confidence intervals of lake level was less than ±10 logs·km⁻¹, which was less than 4% of the total observed CWH fluctuation in our study.

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