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ARTICLE

Coarse woody habitat does not predict largemouth bass young of year mortality during the open-water season

Jacob P. Ziegler, Colin J. Dassow, Stuart E. Jones, Alexander J. Ross, and Christopher T. Solomon

Abstract: Littoral structure is often assumed to provide refuge to young of year (YOY) freshwater fish species, but empirical in situ tests of this relationship are lacking. We estimated mortality rates of YOY largemouth bass (*Micropterus salmoides*) over the open-water season in 13 lakes in northern Wisconsin and Michigan using repeated snorkel surveys. Our goal was to test the hypothesis that mortality rate is negatively related to the abundance of littoral coarse woody habitat, which ranged from 3 to 1500 pieces of wood per kilometre of shoreline in these lakes. Instantaneous mortality rates were well-constrained and ranged from 0.04 to 0.19 among the 13 lakes. Mortality was not related to coarse woody habitat abundance. Our results suggest that the relationship between coarse woody habitat and YOY mortality might not be as strong or universal as is often assumed.

Résumé : Il est souvent tenu pour acquis que la structure littorale fournit des refuges aux jeunes de l'année d'espèces de poissons d'eau douce, mais des tests empiriques in situ pour vérifier cette relation sont insuffisants. Nous avons estimé les taux de mortalité d'achigans à grande bouche (*Micropterus salmoides*) jeunes de l'année durant la période d'eau libre dans 13 lacs du nord du Wisconsin et du Michigan, en utilisant des relevés de plongée en apnée répétés. L'objectif était de vérifier l'hypothèse selon laquelle le taux de mortalité est négativement relié à l'abondance d'habitats littoraux à matériaux ligneux grossiers, qui contiennent de 3 à 1500 morceaux de bois au km de rive dans ces lacs. La fourchette de taux de mortalité instantanés a été bien délimitée, allant de 0,04 à 0,19 dans ces 13 lacs. La mortalité n'était pas reliée à l'abondance d'habitats à matériaux ligneux grossiers. Nos résultats donnent à penser que la relation entre les habitats à matériaux ligneux grossiers et la mortalité des jeunes de l'année peut ne pas être aussi forte ou universelle que ce qui est souvent tenu pour acquis. [Traduit par la Rédaction]

Introduction

Young of year (YOY) mortality is an important determinant of population dynamics, and minimizing YOY mortality can increase productivity and resilience of fish populations. Literature reviews of experiments focused on mortality in stage-structured populations provide empirical evidence that changes in YOY mortality have significant and often counterintuitive effects on population abundance (Zipkin et al. 2009; Schröder et al. 2014). In a theoretical study, Carpenter and Brock (2004) illustrated that reducing YOY mortality in lakes had the combined effect of increasing the level of harvest a fish stock can withstand before collapsing and decreasing the benefits anglers receive from overfishing. Additional theoretical studies have demonstrated that freshwater fish species with higher YOY mortality require larger population sizes to persist (Velez-Espino and Koops 2012), and that population growth rates for most freshwater fish species are more sensitive to YOY mortality than adult mortality (Van der Lee and Koops 2016). Population level outcomes of YOY mortality can affect community level outcomes through Allee, emergent facilitation, predator exclusion, and cultivation effects (Walters and Kitchell 2001; Persson and de Roos 2013). However, YOY mortality estimates of freshwater fish species are rare, and those that span environmental gradients, which build intuition of how YOY mortality might vary with environmental change, do not exist.

Much of the research to date on controls of early-life mortality and recruitment of freshwater fish species has ignored mortality during the open-water season, instead focusing on body size and the advantages it confers for overwinter survival. Early studies investigating controls of YOY mortality were conducted in systems without top predators (Ludsin and DeVries 1997; Post et al. 1999; Pine et al. 2000) or only considered overwinter mortality (Post and Evans 1989; Miranda and Hubbard 1994*a*, 1994*b*). These studies provided evidence that YOY with larger body sizes had lower overwinter mortality, likely due to an increased foraging ability and higher fat stores (although see Rogers and Allen 2009 who did not detect an effect of size-dependent overwinter mortality). However, body size is largely determined by hatch date and growth rates (Miller et al. 1988), variables that are difficult for fisheries managers to control.

Open-water season YOY mortality has been largely ignored in studies, but there is some evidence that it is a determinant of recruitment success in largemouth bass. Like research on YOY mortality in general, much of the focus of largemouth bass YOY mortality has been on the potential for increased body size to decrease overwinter mortality (Miller and Storck 1984; Miranda and Muncy 1987; Miranda and Hubbard 1994*a*, 1994*b*; Olson 1996; Garvey et al. 1998; Pine et al. 2000). During the open-water season, however, Rogers and Allen (2009) found no effect of body size on largemouth bass YOY mortality. While Rogers and Allen (2009) were unable to compare the relative importance of overwinter mortality to open-water season mortality, Post et al. (1998) found that the open-water season represented a more extreme bottleneck for largemouth bass YOY survival than overwinter survival. In addition, Post et al. (1998) found that estimates of YOY predation during the open-water season explained 98% of the variation

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Table 1. Study lake information and young of year mortality model estimates.

Lake	Year	Latitude	Longitude	CWH (no.·km^{-1} of shoreline)	Area (km^2)	Littoral area (km^2)	z (YOY inst. daily mort.)	X_0 (ln initial YOY ab.)	k (neg. binom. dispersion)
Johnson	2017	45.90	−89.72	2.5	0.35	0.21	0.19 (±0.09)	3.55 (±1.01)	0.010 (±0.009)
Little Crawling Stone	2017	45.92	−89.90	2.5	0.47	0.34	0.14 (±0.09)	3.09 (±3.78)	0.010 (±0.007)
Arrowhead	2017	45.91	−89.69	17	0.40	0.30	0.08 (±0.02)	4.90 (±0.76)	0.10 (±0.02)
Morton	2016	46.19	−89.58	23	0.70	0.50	0.08 (±0.02)	2.17 (±0.54)	0.16 (±0.04)
McCullough	2016	46.20	−89.57	100	0.93	0.31	0.09 (±0.03)	2.63 (±0.56)	0.05 (±0.02)
Erickson	2017	45.95	−89.62	140	0.47	0.30	0.04 (±0.02)	1.18 (±0.32)	0.7 (±0.3)
Elbow	2017	46.35	−89.78	430	0.11	0.14	0.10 (±0.03)	4.40 (±0.63)	0.16 (±0.04)
Redboat	2017	46.34	−89.77	530	0.11	0.13	0.12 (±0.05)	5.12 (±0.96)	0.020 (±0.008)
Eel	2017	46.30	−89.76	660	0.23	0.48	0.10 (±0.09)	5.33 (±2.76)	0.010 (±0.004)
Paul	2016	46.25	−89.50	800	0.016	0.03	0.05 (±0.01)	2.87 (±0.27)	0.21 (±0.05)
East Long	2016	46.24	−89.50	830	0.033	0.02	0.16 (±0.08)	2.07 (±1.97)	0.02 (±0.01)
West Long	2016	46.24	−89.50	830	0.054	0.07	0.12 (±0.04)	3.39 (±3.91)	0.02 (±0.01)
Thrush	2017	46.32	−89.79	1500	0.32	0.13	0.14 (±0.06)	4.99 (±0.84)	0.020 (±0.007)
Range				2.5–1500	0.016–0.93	0.7–1.8	0.04–0.19	1.18–5.33	0.01–0.7

Note: 95% confidence intervals are provided in parentheses, YOY = young of year, CWH = coarse woody habitat, inst. daily mort. = instantaneous daily mortality, ab. = abundance, and neg. binom. = negative binomial. Note, initial YOY abundances reported in natural log. Littoral area was calculated as shoreline perimeter × average length from shore where sediment light was 1% surface light (determined from littoral slope and Secchi depth).

in observed initial YOY densities, suggesting that nearly all YOY mortality during the open-water season was due to predation.

Coarse woody habitat is generally assumed to reduce YOY predation and mortality rates in temperate lakes by providing refuge from predators, but empirical tests of this hypothesis have yielded mixed results. Fish species are frequently found in littoral structure like coarse woody habitat and submerged macrophytes during their early-life stages (Hall and Werner 1977; Wallus and Simon 2008; Lewin et al. 2004), which has led to the assumption that this habitat is used as refuge (MacRae and Jackson 2001; Wallus and Simon 2008; Roth et al. 2007; Biggs et al. 2009; Ziegler et al. 2017). However, DeBoom and Wahl (2013) found no effect of coarse woody habitat abundance on predation of YOY of two species in mesocosm experiments, and Klecka and Boukal (2014) found that littoral structure can be used as an ambush site by some predators. Alternatively, in an overwinter pond experiment Miranda and Hubbard (1994*a*) found that coarse woody habitat provided refuge from mortality for the smallest of four size classes of YOY largemouth bass, indicating an interaction between starvation and predation vulnerability, and Sass et al. (2006*a*) found that yellow perch experienced a recruitment failure after a whole lake removal of coarse woody habitat. They attributed the recruitment failure to increased predation pressure on YOY yellow perch and lack of spawning substrate.

The assumption that littoral structure is refuge for YOY has led aquatic and fisheries researchers to suspect that a threshold of coarse woody habitat exists, below which fish populations experience adverse effects from increased YOY mortality (Carpenter and Brock 2004; Liu et al. 2007). Coarse woody habitat is sensitive to human development and, often completely absent when there are more than seven houses per kilometre of shoreline (Marburg et al. 2006; Liu et al. 2007). The assumption that YOY mortality is affected by coarse woody habitat, and in turn by housing development, has been included in many studies of littoral species (Brock and Carpenter 2007; Biggs et al. 2009; Ziegler et al. 2017). However, there have been no comparisons of YOY mortality among lakes across gradients of coarse woody habitat density. In situ mortality estimates can provide insights into factors regulating recruitment success to help guide sustainable development and fisheries management.

In this study, we tested for a relationship between littoral habitat structure and YOY mortality during the open-water season by estimating largemouth bass YOY mortality rates in 13 lakes that varied in coarse woody habitat density. Based on the prevalent hypothesis that coarse woody habitat reduces predation pressure on YOY, we predicted that coarse woody habitat would be negatively correlated to YOY mortality.

Methods

Study sites

We selected 13 small lakes in northern Wisconsin and the Upper Peninsula of Michigan, USA, that had largemouth bass as the dominant piscivore and which spanned previously documented coarse woody habitat gradients (Table 1). Development in this lake-rich forested region has been rapid since the 1940s and is often concentrated around lakes (Carpenter et al. 2007). As a result there are various degrees of lakeshore development in the region, resulting in a range of coarse woody habitat in lakes (see videos in Supplementary data[1] for what the littoral zone of a lake with high coarse wood habitat density looks like in this region). Littoral coarse woody habitat has been observed to vary from 0 to 965 pieces of wood per kilometre of shoreline in this region (Christensen et al. 1996; Marburg et al. 2006). Our study lakes extended this gradient to 3–1520 pieces of wood per kilometre of shoreline (Table 1).

YOY mortality

We estimated YOY largemouth bass instantaneous mortality rates in each lake using the decline in YOY relative abundance over the open-water season, following the methods of Essig and Cole (1986) and Miranda and Hubbard (1994*b*). We estimated relative abundance on at least four occasions in each lake, at approximately biweekly intervals from the beginning of June (just after swim-up) until late August or early September of 2016 or 2017 (Table 1). In both years largemouth bass successfully produced cohorts, and when we returned in 2017 to lakes that had been sampled in 2016 we did not observe major differences in bass recruitment between the two years. There were no notable events that would cause recruitment failures during our study period (e.g., anoxia, algal blooms, or large decreases in water level or temperature). We used line-transect snorkel surveys similar to Weidel et al. (2007) and Chamberland et al. (2013) to quantify relative abundance. We determined through a pilot study in our lakes that electrofishing was not effective at capturing YOY in the spring and early summer, while snorkel surveys allowed for con-

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0050.

sistent quantification of YOY throughout their first open-water season and did not affect YOY mortality, unlike electrofishing and rotenone sampling (Chamberland et al. 2013). Numerous studies have shown strong correlations (R^2 between 0.88 and 0.99) between snorkel survey counts and absolute abundances of littoral fish in both lakes and rivers (Mullner et al. 1998; Pink et al. 2007; Weidel et al. 2007; Chamberland et al. 2013) and Brind'Amour and Boisclair (2004) found no difference between relative abundance estimates of lake littoral fish when measured using snorkel surveys or beach seines.

Relative abundance estimates are an accurate measure of the decline in YOY if detectability of YOY does not change within a lake over time. We controlled for and estimated habitat related detectability in our sampling, and we tested for potential biases in YOY detection due to changes in water clarity. We always returned to the same sites and transects in each lake to maintain the same littoral structure density on transects over the sampling period. Within lakes, we tested for an effect of coarse woody habitat on YOY detection probability using well-developed theory from species occupancy modeling (MacKenzie et al. 2002). We calculated the site level detection probability of YOY using logistic regression with eight observations of YOY presence or absence on transects at each of the six sites per lake and sampling day (see Mollenhauer et al. 2018 for spatial resampling method of MacKenzie et al. 2002). Transect level coarse woody habitat density was included as a predictor of site level variation in YOY detection probability. We compared logistic regression models that allowed the effect of coarse woody habitat on YOY detection probability to remain constant or vary among sites and over time using Akaike's information criterion (AIC_c). Similar to Toft et al. (2007), we measured water clarity at the time of sampling as a covariate of visual detectability to determine if it changed over time. We measured water clarity as horizontal Secchi distance, vertical Secchi depth, and percent cloud cover. We also looked for changes in behavioural responses of YOY largemouth bass to divers over the study period, and we considered potential biases in our results related to increased fish length over time (see Supplementary data[1]).

On each lake visit we conducted snorkel surveys at six littoral sites located at the north, northeast, east, south, southwest, and west edges of the lake. At each site we sampled eight 10 m transects that extended perpendicular from shore, because YOY largemouth bass are littoral (Wallus and Simon 2008) and transect orientation should be perpendicular, rather than parallel, to the density gradient of the object of interest (Buckland et al. 1993). We marked the end of transects on the shoreline with flagging tape and the start from a boat using a buoy and a range finder, being careful never to disturb transects. Two divers entered the water approximately 30 m from transects, approached each transect slowly and calmly, swam in parallel at a constant rate of 10 m per minute, and recorded on underwater tablets the number of YOY largemouth bass within their line of sight. It is common methodology to estimate school size when there are more fish than divers can count; we improved on this methodology by using video analysis to provide reproducible, unbiased, and more accurate counts of YOY when there were more than five YOY present on a transect (Buckland et al. 1993). Each underwater transect was filmed using a GoPro Hero 4 (GoPro Inc., San Mateo, California, USA), and in instances where more than five YOY were encountered on a transect, all YOY were captured on video and then video frames were used to count individuals using the cell counter plugin on ImageJ 1.x (Schneider et al. 2012; De Vos 2010). While using video counts might change the detection probability of YOY compared with only using snorkel counts, any bias introduced here is likely to be much smaller than simply estimating school size, as is standard practice in snorkel surveys. Videos typically had good visibility allowing for easy counting of YOY present in video frames.

We conducted additional line-transect samples in pelagic habitat in each lake to confirm the absence of significant ontogenetic habitat shifts that could have biased the mortality rates that we estimated from our littoral sampling. We sampled at three sites per visit just offshore of littoral sites. The total amount of pelagic sampling varied per lake but was conducted at least twice (once early in the season and once later in the season) and on average three times per lake over the sampling period. We set 40 m pelagic transects parallel to shore at 30 and 40 m from shore, using a thin white nylon line set at half the thermocline depth. If the thermocline depth was greater than 2 m, scuba divers swam along the transect line at a speed of 10 m per minute and recorded YOY largemouth bass in the same manner as littoral transects. If the thermocline depth was less than 2 m and divers could see past 2 m in the water column (judged by vertical Secchi depth), the pelagic transects were snorkeled in the same manner as littoral transects.

Littoral structure

We determined the density of coarse woody habitat, the structural complexity of coarse woody habitat, and the density of macrophytes, another form of littoral structure, in each of our study lakes. Coarse woody habitat density was previously estimated for eight of our study lakes by Marburg et al. (2006), and we estimated coarse woody habitat in our other five lakes using their methods. We also estimated coarse woody habitat density in all 13 lakes by quantifying the number of pieces of wood present on our littoral transects from video footage. Our video-derived estimates of coarse woody habitat density were strongly correlated with the estimates from Marburg et al. (2006) (r = 0.92, p < 0.01, n = 6), so we present only the latter here. We used video footage to estimate the mean branchiness of woody habitat (following the methods of Marburg et al. 2006) and percent macrophyte cover.

Statistical analyses

The expected size of a population X at time t undergoing a random death process is given by a negative exponential model with initial abundance X_0 and mortality rate z (Bailey 1990), with errors that might be distributed with Poisson or negative binomial distributions (Bolker 2008):

$$(1) \qquad X_t \sim \text{Poisson}\left(X_0 e^{-zt}\right)$$

or

$$(2) \qquad X_t \sim \text{Negative Binomial}\left(X_0 e^{-zt}, k\right)$$

We estimated the initial abundance (X_0), mortality rate (z), and the dispersion parameter (k, eq. 2 only) along with their 95% confidence intervals for all 13 lakes by fitting our count data over time to eqs. 1 and 2 using maximum likelihood (Table 1 and Fig. 1). We compared fitted models relative to each other with small-sample size corrected AIC_c. All statistical analyses were conducted in R using packages MASS and AICcmodavg (Venables and Ripley 2002; R Core Team 2017; Mazerolle 2017).

To test for potential effects of coarse woody habitat density, coarse woody habitat complexity, and the density of macrophytes on YOY mortality we used ordinary least-squares regression and weighted least-squares regression, with mortality estimates (z in eqs. 1 and 2) as the dependent variable and coarse woody habitat and littoral structure as the predictor variables (Fig. 2). In weighted least-squares regression we weighted mortality estimates by the inverse of their squared standard errors (Chatterjee and Hadi 2015). For simplicity, all results presented in figures are from models that had a single predictor of YOY mortality; however, we tested all predictor variables individually and in combination with each other, including interactions (Supplementary data,

Fig. 1. An example of young of year (YOY) largemouth bass counts per 10 m transect line over the study period for a single lake (see Supplementary data, Fig. S2[1] for plots from all lakes). Individual points represent total number of YOY present on a 10 m transect line and are jittered to prevent over plotting (sampling days were 0, 7, 25, 38, and 49). The solid line shows the fit of the model used to estimate YOY mortality (a negative exponential model with negative binomial errors). Note that the *y* axis is in logarithmic scale.

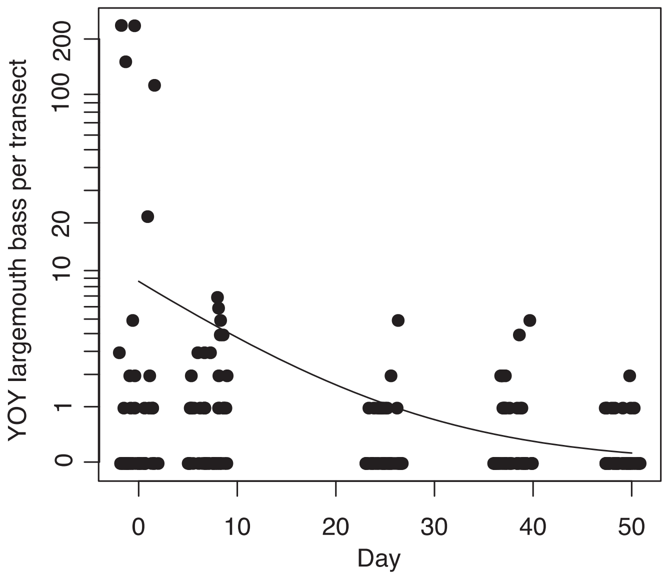


Table SII[1]). When an estimated dependent variable (EDV) is used in regression it can violate assumptions of heteroscedasticity because of variation in the EDV's 95% confidence intervals (Hanushek 1974; Williams and Lewis 2008). Two approaches are frequently used to deal with EDV regression: ordinary least-squares and weighted least-squares (Williams and Lewis 2008; Chatterjee and Hadi 2015). Ordinary least-squares regression (OLS) allows some of the error in the regression model to be unexplained by predictor variables but does not account for known variation in measurement error when estimating regression parameters and standard errors. Weighted least-squares regression (WLS) does not allow unexplained variation from predictor variables (i.e., it assumes all of the error in the regression model is due to measurement error and R^2 would be 1 if the EDV were directly observable) but accounts for measurement error in the EDV when fitting regression parameters and standard errors. Therefore, we report both OLS and WLS results as recommended by Williams and Lewis (2008). In all instances, we plotted the 95% confidence intervals from the WLS regression fits as they accounted for uncertainty in mortality parameter estimates.

When testing for an effect of littoral structural complexity on YOY mortality we could not include coarse woody habitat density and mean coarse woody habitat branchiness in the same model because they were positively correlated (r = 0.84, p < 0.01). Therefore, to characterize total littoral structure, we ran a principal component analysis, which explained 94% of the variation in coarse woody density, coarse woody branchiness, and macrophyte cover in two principal components (PC1 and PC2 in Table 2). We then used the principal components, which corresponded to coarse woody habitat complexity (PC1) and macrophyte cover (PC2), as predictor variables of YOY mortality following the same methods as above.

Our hypothesis assumes that predation pressure is a strong control of YOY mortality in our lakes, as has been demonstrated in previous studies (Anderson 1988; Duarte and Alcaraz 1989; Post and Evans 1989; Ludsin and DeVries 1997; Post et al. 1998; 1999; Post and Parkinson 2001). We used historical data on predator densities in a subset of our lakes to corroborate this assumption (see Supplementary data, Sect. I[1]).

Results

YOY mortality

YOY counts significantly and exponentially declined over the study period in all lakes (Fig. 1). On average, we sampled 4.6 km of transect per lake and observed 4400 YOY per lake over the study period. For all lakes, a negative exponential – negative binomial model fit our observed count data better than a negative exponential – Poisson model (in all instances ΔAIC > 100). YOY largemouth bass mortality estimates in the 13 lakes ranged from 0.04 to 0.19 with a mean of 0.11 and a standard deviation of 0.04, and had reasonably well-constrained confidence intervals (Table 1).

Our ability to detect YOY was for the most part unrelated to coarse woody habitat density, and water clarity did not significantly vary over time. There was no significant effect of CWH on YOY detection probability in 11 of our 13 lakes (Fig. 3). In one lake, the effect of coarse woody habitat significantly varied by site and had a significant positive effect on detection probability in two sites (West Long in Fig. 3, ΔAIC_c from a model with constant site effect > 2). Coarse woody habitat had a significant negative effect on YOY detection probability in only one lake, but this lake had the lowest coarse woody habitat density of all lakes (Fig. 3, Johnson Lake). Therefore, it is likely that the decline in detection probability with coarse woody habitat observed in Johnson Lake was ecologically driven rather than determined by a diver's reduced ability to see YOY when coarse woody habitat was present. In all lakes, the effect of coarse woody habitat on site level YOY detection probability did not vary over time, as our best model predicting site detection probability included a constant coarse woody habitat effect over time for all lakes (Fig. 3, ΔAIC_c > 50 compared with model with coarse woody habitat effect varying by lake, site, and time). Water clarity in each lake at the time of sampling did not significantly change over the study period when measured as horizontal Secchi distance (p values for the day of year effect in a regression model with lake as a blocking factor were all greater than 0.05 for all lakes) and vertical Secchi depth (all p > 0.05). Cloud cover at the time of sampling did not significantly change over the study period (all p > 0.05).

The declines in YOY counts were not due to ontogenetic shifts from littoral to pelagic habitats. We did not detect YOY largemouth bass on pelagic transects in 9 of our 13 lakes, despite an average 740 m of pelagic transect line sampling per lake over the study period. In two lakes, YOY were present on pelagic transects only where those transects were as shallow or more shallow than the littoral transects (i.e., not representative of pelagic habitat but rather additional littoral habitat). In the remaining two lakes, a negative exponential – negative binomial model described the decline in pelagic YOY counts over the open-water season, and the pelagic mortality estimates did not significantly differ from littoral mortality estimates (mortality parameter estimate and 95% CI for pelagic YOY counts: $z = 0.05 \pm 0.02$ and $z = 0.07 \pm 0.03$, mortality parameter estimate and 95% CI for littoral YOY counts: $z = 0.05 \pm 0.02$ and $z = 0.08 \pm 0.02$, respectively). Therefore, it is unlikely that movement of YOY to pelagic habitat could account for the significant decline in littoral YOY counts in our lakes, as pelagic YOY were either not present or, when they were present, declined at the same rate in both habitats.

Littoral structure and YOY mortality

In our 13 lakes, which spanned a large coarse woody habitat gradient (3–1500 pieces of wood per kilometre of shoreline), YOY mortality was unrelated to coarse woody habitat, coarse woody habitat complexity, and macrophyte cover (Figs. 2 and 4; Supple-

Fig. 2. YOY largemouth bass mortality was not significantly related to coarse woody habitat density (A), coarse woody habitat complexity (B), or macrophyte cover (C). The first principal component (PC1) from a principal component analysis describing littoral structural complexity was positively correlated to coarse woody habitat density and branchiness, while the second principal component (PC2) was positively correlated to macrophyte cover (Table 2). Models were fit with weighted-least squares) regression and ordinary least-squares regression. Vertical lines represent 95% confidence intervals for mortality estimate fits (z parameter in eq. 2). The shaded area is the 95% confidence interval from a weighted least-squares (WLS) regression models.

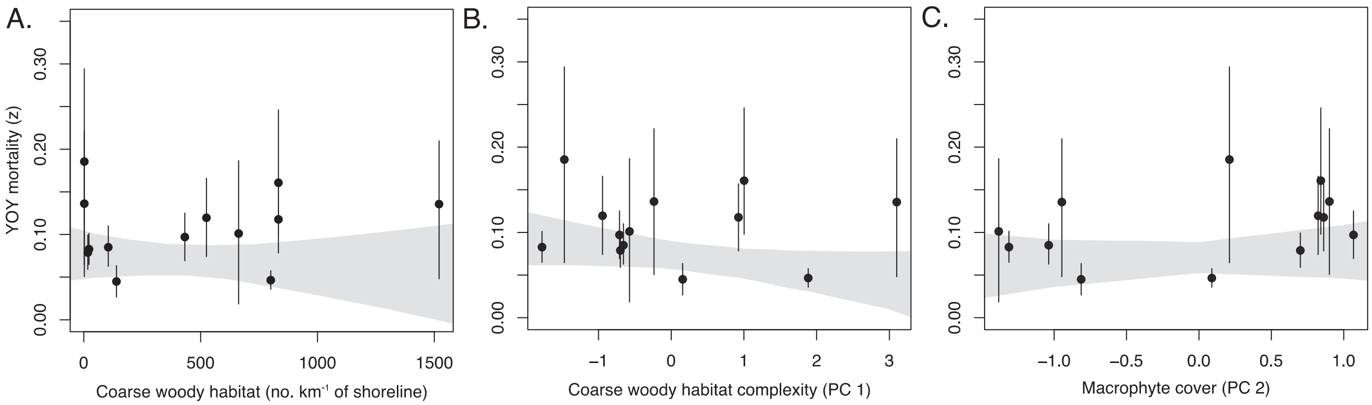
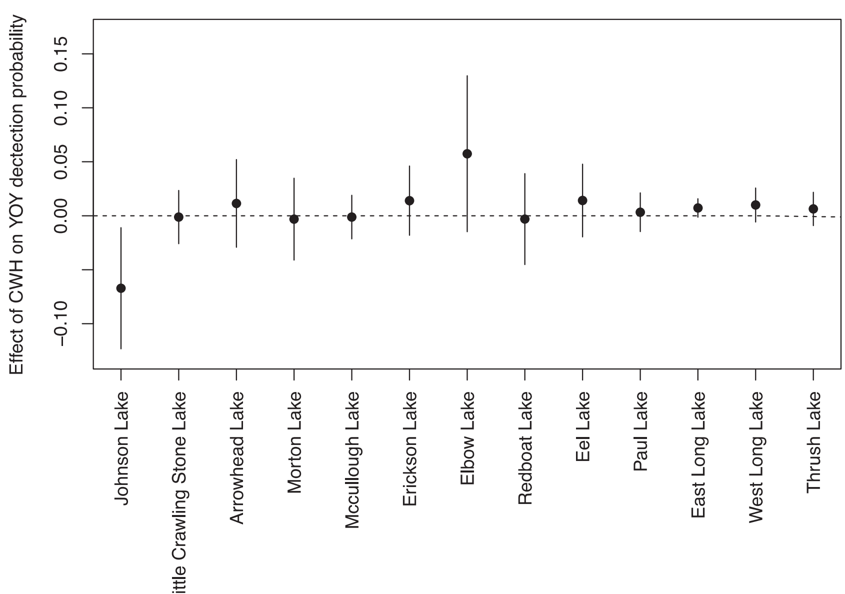


Table 2. Description of littoral structure principal components.

Littoral structure	PC 1	PC 2
Coarse woody habitat complexity		
Number per kilometre of shoreline	$\mathbf{r = 0.93, p < 0.001}$	$r = 0.10, p = 0.75$
Mean branchiness	$\mathbf{r = 0.85, p < 0.001}$	$r = 0.40, p = 0.17$
Macrophyte cover		
Percentage cover	$r = 0.51, p = 0.07$	$\mathbf{r = 0.85, p < 0.001}$
Variance explained	0.62	0.30

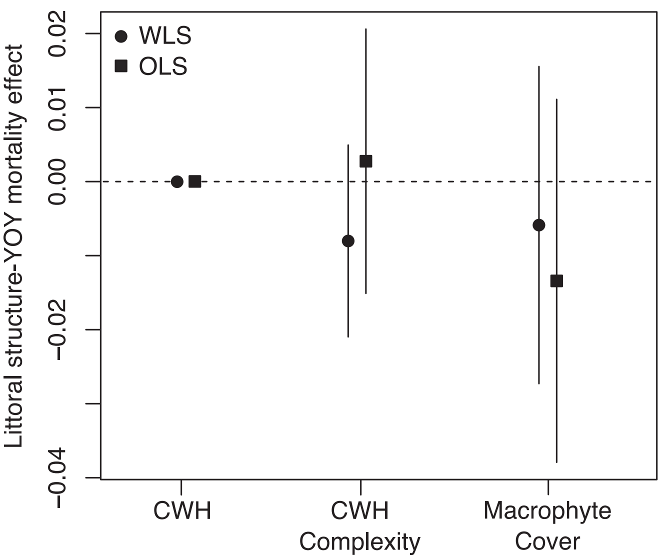
Note: Correlations show the relationship of the number of pieces of wood per kilometre of shoreline, mean branchiness of coarse woody, and percent macrophyte cover with two principal components from a principal component analysis that explains 92% of the variation in these three variables. Significant correlations are highlighted in bold.

Fig. 3. Detection probability of YOY was unrelated to coarse woody habitat (CWH) on transects in 11 of our 13 lakes. In two lakes (Johnson and West Long) there were significant effects but these were weak and in opposite directions. Note, the best model explaining West Long YOY detection probability included an effect of CWH that varied by site (two sites had significantly positive effects while the rest were not significant), but here we display the lake level effect. In all lakes the best model included a constant CWH effect over time.



mentary data Table SI[1]). Mortality was not significantly related to coarse woody habitat in WLS or OLS models (Fig. 2A; Supplementary data Table SI[1]). Our data constrained the effect of coarse woody habitat on YOY mortality to near zero (Fig. 4). Coarse woody structural complexity and macrophyte cover (Table 2, PC1) were also poor predictors of YOY mortality during the open-water season and were not significant in any WLS or OLS models (Figs. 2B and 3C; Supplementary data Table SI[1]).

Fig. 4. The effect of CWH on YOY mortality was near zero, while CWH complexity and macrophyte cover had more variable effects on YOY mortality but were not significantly different from zero. The effects fit with weighted least-squares (WLS) regression and ordinary least-squares (OLS) regression were similar. Vertical lines represent 95% confidence intervals (the lines for CWH are indistinguishable from the size of points).



Discussion

Our results are, to our knowledge, the first to compare in situ YOY mortality along an environmental gradient in lakes and suggest that the relationship between coarse woody habitat and YOY mortality might not be as strong or universal as is often assumed. Although our results are limited in sample size and only consider one freshwater fish species, they suggest that littoral structure variations alone may not lead to decreased YOY mortality as is often assumed in the literature (MacRae and Jackson 2001; Wallus and Simon 2008; Roth et al. 2007; Biggs et al. 2009; Allen et al. 2011). Our results also advance our understanding of early-life mortality of largemouth bass over the open-water season and provide an example that can be used to better understand early-life mortality and its determinants in other species through well-constrained estimates of YOY mortality.

Our estimates of open-water season YOY mortality are comparable to the few estimates that exist for largemouth bass and suggest that open-water season mortality is greater than overwinter mortality. There are only three published estimates of YOY largemouth bass open-water season mortality that we are aware of (Miranda and Hubbard 1994*b*; Shirley and Andrews 1977; Rogers and Allen 2009). Only two studies provided instantaneous mortality estimates: Shirley and Andrews (1977) provided one without an error estimate ($z = 0.0028$) making it difficult to compare with our estimates, while Rogers and Allen (2009) had six estimates with a range of 0.019 to 0.12. Our instantaneous mortality rates were well-constrained and ranged from 0.04 ± 0.02 to 0.19 ± 0.09 among 13 lakes, which is similar to the range observed by Rogers and Allen (2009). Rogers and Allen (2009) found that open-water season mortality alone was as high or higher than overwinter mortality. Our range in estimates of open-water season mortality are higher than those reported for largemouth bass overwinter mortality (range in estimates from Garvey et al. 1998 and Miranda and Hubbard 1994*a* = 0.00008 to 0.04). Despite the focus in the literature on overwinter mortality and its implications for recruitment success, our results suggest that open-water season mortality should be as great or greater a concern for recruitment success than overwinter mortality in largemouth bass.

High open-water season YOY mortality in largemouth bass could have a compensatory effect at the population level, especially when cannibalism is high, by reducing density-dependent competition of YOY for resources. A Ricker stock–recruitment relationship predicts that recruitment should decline at higher adult population densities if there is cannibalism by adults (Ricker 1954). Despite cannibalism accounting for the majority of largemouth bass YOY mortality in Post et al. (1998), they found no relationship between adult density and recruitment success. One explanation for this is that self-thinning through cannibalism may remove density-dependent mortality that YOY might otherwise experience and compensate for increased predation pressure at higher adult densities. Based on our range of mortality rates (0.04 ± 0.02 to 0.19 ± 0.09) and study duration, largemouth bass populations can lose between 68% and 99% of their YOY populations over the open-water season. These large declines in abundance, most likely caused by predation pressure (see Supplementary data, Sect. I[1]), would reduce competition among the remaining YOY for resources and improve their chance for successful recruitment to older life stages.

While littoral structure may not serve as refuge for YOY largemouth bass, researchers have hypothesized that it is refuge to other freshwater species. For example, YOY rainbow trout (*Oncorhynchus mykiss*; Tabor and Wurtsbaugh 1991), yellow perch (*Perca flavescens*; Eklöv 1997), and walleye (*Sander vitreus*; Pratt and Fox 2001) have been assumed to use littoral structure to reduce predation pressure. However, few empirical test have provided evidence for this (Savino and Stein 1982; Tabor and Wurtsbaugh 1991; Sass et al. 2006*b*). Behavourial differences in boldness of species may explain why largemouth bass do not receive refuge from littoral structure, but species like bluegill (*Lepomis macrochirus*), that adapt their behavour to predators, do (Savino and Stein 1982; Turner and Mittelbach 1990). There is a known trade-off of boldness in largemouth bass, bold juveniles experience increased predation mortality but bold adults experience higher fitness and pass on their heritable behavioural trates (Ballew et al. 2017). Other known predictors of recruitment success among species are climate change, lake morphometry, overharvesting, and spawning substrate (Nash et al. 1999; Walters and Kitchell 2001; Hansen et al. 2015) but without well-controlled studies estimating YOY mortality, the relative importance of these predictors and their interactions remains unclear.

Our analysis demonstrates how well-constrained mortality estimates can advance our understanding of determinants of freshwater fish early-life mortality and recruitment success. Our approach, while time-intensive (65 days of snorkel surveys for 13 mortality estimates) might be useful in similar studies of littoral species in small lakes. Our approach might also be powerfully combined with large-scale experiments; for instance, one could manipulate wood levels and measure YOY mortality response in a whole-lake, before–after control–impact design. Other promising approaches for understanding determinants of YOY mortality in multiple systems include using marked stocked YOY (Shirley and Andrews 1977), standardized long-term monitoring of YOY over the open-water season among multiple lakes (Post et al. 1998), and meta-analyses.

Fisheries management focused on maintaining productive fish stocks requires knowledge of critical variables like YOY mortality and how they might change with habitat modifications such as removal or addition of littoral structure. Thresholds of critical variables that can lead to undesirable changes in social–ecological systems are a key concept in resilience thinking (Folke 2016). Understanding where these critical thresholds lie and avoiding trajectories that cross them is the role of responsible natural resource management. The concept of a safe operating space bounded by critical thresholds has recently been applied to fisheries management and illustrates the necessity of understanding which critical variables a manger can control and how best to allocate effort in managing them (Carpenter et al. 2017). For example, federal fisheries management in Canada has shifted from protecting fish habitat to protecting fish productivity, which requires a better understanding of the effects that habitat alterations have on critical variables for fish productivity such as YOY mortality (Rice et al. 2015). Our results provide useful but rare estimates of in situ YOY mortality along a littoral structure gradient and suggest that littoral structure may not be as strong or universal a control on open-water season YOY mortality as is often assumed.

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