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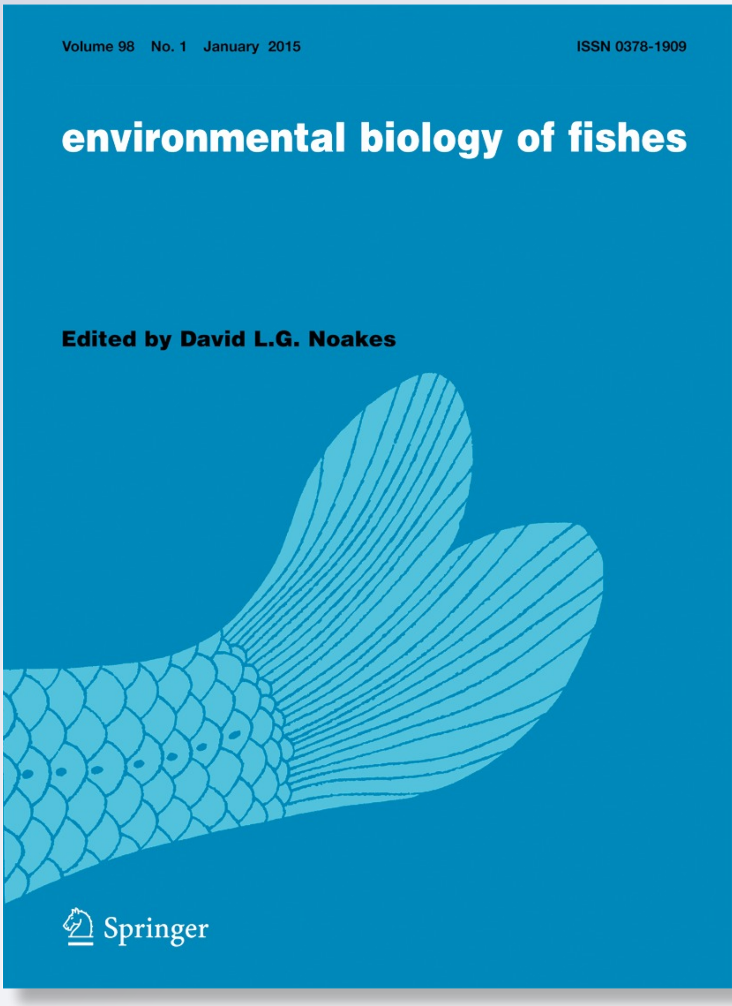

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Quantifying brood predation in Largemouth Bass (*Micropterus salmoides*) associated with catch-and-release angling of nesting males

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Abstract Largemouth Bass (*Micropterus salmoides*) is a highly popular and widely exploited sport fish that provides paternal care to its offspring during the reproductive season each spring. During a catch-and-release angling event, brood predators (e.g. genera *Lepomis* and *Ambloplites*) can enter Largemouth Bass nests and consume embryos, reducing the parental male's reproductive success. While the negative impacts of angling nesting bass have been well documented, factors affecting the rate at which embryos are consumed by nest predators have not been studied at either the individual or population scale. We conducted field observations in nine lakes in southeastern Ontario and southwestern Quebec with abundant Largemouth Bass populations and varying brood predator densities to assess what factors affect how quickly brood predation begins once the male is removed, how quickly a male returns to his nest after release, and which males abandon their nests. Brood predator densities varied among lakes, and when predation occurred (65 % of all nests), it began sooner after the male was angled in nests with higher densities of brood predators nearby. The mean return time of a male was 30.0 min after being held in a live well for 15 min. The mean consumption rate (on a per-predator basis) for all nests that experienced predation was 20.9 free swimming fry predator^{-1} min^{-1}, and the rate was higher in nests with higher mating success. The number of free swimming fry consumed was positively correlated with brood predator densities near the nest prior to angling, and the change in brood size was predictive of whether the male abandoned its nest. Predator density, parental male quality, and mating success were not associated with differences in abandonment decisions.

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Introduction

Largemouth Bass (*Micropterus salmoides*) is a highly popular and widely exploited sport fish (Barnhart 1989; Noble 2002) that provides paternal care to its offspring during the reproductive season each spring (Neves 1975). Angling effort targeting Largemouth Bass is often higher during the spring spawning season relative to the rest of the angling season (Einhouse et al. 2002), and the aggressive nature of parental male Largemouth Bass while providing parental care (Ongarato and Snucins 1993) increases their vulnerability to angling (Lindgren and Willis 1990). Whether harvested or released, angling the nest-guarding male provides brood predators the opportunity to enter the nest and consume all or some of the embryos (Kieffer et al. 1995; Steinhart et al. 2004), reducing that male's individual reproductive success and often triggering abandonment of the brood (Philipp et al. 1997; Zuckerman and Suski 2013). Several studies indirectly related the likelihood of abandonment to nest exposure time (Philipp et al. 1997; Suski et al. 2003; Hanson et al. 2007), but only two studies have provided direct evidence that brood loss is an important signal to a returning male bass that is associated with its decision to continue to defend the remaining brood or abandon the nest entirely (Suski and Philipp 2004; Zuckerman and Suski 2013).

Although potential brood predators such as Bluegill (*Lepomis macrochirus*), Pumpkinseed (*L. gibbosus*), and Rock Bass (*Ambloplites rupestris*) are common in systems with Largemouth Bass, the impact of predator densities on the likelihood of predation has rarely been quantified (Gravel and Cooke 2009). No study to date has empirically determined the instantaneous consumption rate of brood predators, nor has the relationship between predation intensity, nest exposure time, and brood loss been evaluated in a single experiment. Therefore, a better understanding of how brood consumption rates, predation risk, and time of nest exposure combine to predict the level of brood loss is needed to design effective management strategies for protecting spawning bass and reducing abandonment rates.

This study examines how male parental qualities (size, vigilance and aggression), predator density, and mating success (brood size) are related to nest predation dynamics at the scale of the individual. First, we evaluated the relationship of these three factors on the time to onset of predation once the male is removed. Second, we calculated instantaneous consumption rates to estimate how rapidly brood predators are able to consume embryos. Third, we evaluated how predator density, male parental qualities and mating success related to how quickly a male returns to his nest (return time). Onset of predation, instantaneous consumption rate, and nest exposure time together predict the overall impact of a catch-and-release angling event on brood loss. Lastly, we evaluated the relationship of brood loss, along with predator density, parental qualities, and mating success to the male's decision to abandon its nest after the angling event or to continue guarding it. Understanding brood predation dynamics has important implications for developing management strategies designed to protect spawning bass and to maximize reproductive success and recruitment.

Methods

Study design and data collection

This study was conducted in a series of nine lakes within a single ecoregion (Abell et al. 2008) located in southeastern Ontario and southwestern Quebec that were all closed to angling by the public throughout the course of the study. All study lakes contained natural Largemouth Bass populations, but with varying densities of known brood predators (Table 1), primarily Bluegill, Pumpkinseed, and Rock Bass. During the 2009 spawning season, a snorkeler located 70 largemouth bass nests containing fertilized eggs prior to hatching (<2–4 days old), marked them with a numbered plastic tag, estimated the date of spawn based on development of the embryos (Philipp et al. 1985), and determined mating success by assigning an egg score of 1–5 to each brood (Kubacki 1992; Philipp et al. 1997; Suski et al. 2002, 2003; Suski and Philipp 2004; Hanson et al. 2007; Parkos et al. 2011; Zuckerman and Suski 2013). Egg score, an ordinal measure of mating success, can be used to estimate the number of free swimming fry above a nest 1–2 days after swim-up, and is an indication of future reproductive success (Kubacki et al., in review). Snorkelers were instructed to assign egg scores based on the diameter of the spread of eggs, the patchiness of the distribution of eggs, and the saturation of eggs (i.e., the extent to which eggs were deposited on top of each other) in each nest (Table 2). A subset of all nests from each lake were targeted for inclusion in the study so that nests would be in close enough proximity to each other (but typically not less than 10 m) to allow the snorkeler to make circuitous observations on several nests in the course of several hours between capture by angling and the return of the male to the nest after being released. On the rare occasion when fresh hook wounds (e.g., bruising and/or epithelial damage on or near head and mouth) were observed on a nesting male bass, that individual was excluded from the study to avoid introducing bias by including nests in which a brood may have been preyed upon during an angling event prior to the study.

After marking the nest, the snorkeler took a position approximately 3 m from the nest for 1–2 min to allow the parental male and nearby brood predators to acclimate to the presence of the swimmer. To determine predator density in the vicinity of the nest, the swimmer recorded the number of brood predators within 2 m of the nest at the beginning and end of a 2-min observation period (Gravel and Cooke 2009). Predator density was calculated as the maximum number of predators observed during this period. The parental quality of each nesting male was quantified by evaluating nest defense vigilance and aggression. First, nest defense vigilance

Table 1 Surface area (hectares), latitude and longitude, number of nests, the percentage of nests with predation, and mean (standard error) for predator density (maximum number of predators observed), male total length (mm), aggression scores (number of aggressive behaviors), vigilance scores (possible range 0–240), egg scores (ES) and predation intensity (number of active predators) for nine lakes used in the study

Lake	Surface area (ha)	Latitude Longitude	# nests (% predation)	Predator density	Male TL (mm)	Aggression score	Vigilance score	ES (1–5)	Predation intensity
Charleston	2620	44° 32′ 04″ N 76° 00′ 09″ W	3 (33.3)	0.0 (0.0)	418 (44)	0.7 (0.7)	101 (19)	3.0 (0.6)	3.9 (3.9)
Long	16	44° 31′ 40″ N 76° 24′ 09″ W	6 (33.3)	0.0 (0.0)	389 (23)	6.5 (2.9)	73 (36)	3.7 (0.3)	2.1 (1.9)
Loughborough	1800	44° 26′ 31″ N 76° 25′ 18″ W	11 (63.6)	3.2 (1.1)	349 (10)	2.7 (1.2)	114 (14)	3.1 (0.2)	7.4 (2.4)
Maholey	103	45° 43′ 03″ N 74° 48′ 00″ W	13 (61.5)	0.6 (0.4)	363 (10)	13.3 (1.8)	145 (10)	3.4 (0.2)	2.5 (1.2)
Mills	39	45° 47′ 43″ N 74° 46′ 54″ W	11 (90.9)	9.6 (4.5)	296 (13)	11.4 (2.4)	142 (4)	2.9 (0.4)	8.0 (3.0)
Opinicon	788	44° 33′ 51″ N 76° 19′ 00″ W	13 (76.9)	6.4 (1.8)	350 (8)	9.0 (3.5)	126 (6)	3.7 (0.3)	10.8 (2.7)
Otter	19	45° 48′ 13″ N 74° 47′ 41″ W	2 (50.0)	0.0 (0.0)	294 (26)	10.0 (3.0)	120 (0)	4.5 (0.5)	6.5 (6.5)
Whitefish	64	45° 44′ 52″ N 74° 49′ 30″ W	6 (83.3)	0.0 (0.0)	353 (14)	3.3 (2.3)	127 (5)	3.2 (0.4)	1.9 (1.3)
Wolf	954	44° 40′ 06″ N 76° 28′ 47″ W	3 (0)	1.3 (1.3)	419 (11)	2.0 (1.0)	100 (22)	3.3 (0.3)	0.2 (0.2)

was quantified by recording categorical behaviors of the parental male during the 2-min observation period prior to angling. The snorkeler recorded whether the parental male was "off" the nest (i.e., greater than 0.5 m from the nest and not chasing potential brood predators), "on" the nest (i.e., directly above or within 0.5 m of the nest), or "chasing" (i.e., engaged in some anti-predator behavior). For each second the male was "on" the nest that male's vigilance score was increased by one, for each second the male was "chasing", the vigilance score was increased by two, and for each second the male was "off" the nest, the vigilance score was decreased by one. Male vigilance is dependent on predator density such that males with no predators in the vicinity of the nest will not have the opportunity to "chase" and, as a result, the opportunity to increase their vigilance score by two. Second, to quantify male aggression, a controlled test was used to assess the willingness of each parental male to defend its brood. Each male was presented with a bluegill model that was manipulated by the researcher to mimic nest predation movements, including having the predator model enter the nest, occupy the area immediately above the nest, and make contact with the nest substrate with the model's mouth. During the 1-min aggression test, the snorkeler recorded the number of yawns, rushes, and strikes made at the bluegill model by the parental male, and these were summed to determine the aggression score for that male (Suski and Philipp 2004).

Once pre-angling assessments of predator density, parental male quality, and mating success were completed, the snorkeler moved away from the nest, and two researchers in a boat approached the nest area and angled the male from the nest. Total length (TL) of the male was recorded in mm, and the male was held in a live well for 15 min to conservatively simulate the duration of a catch and release angling event while

Table 2 Characteristics that distinguish each level of the egg scoring system used in the current study. Spread is an indication of the diameter of eggs in a nest, patchiness describes the extent to which eggs are clumped together, and saturation describes the extent to which eggs have been deposited on top of each other

Egg score	Spread (in)	Patchiness	Saturation
1	6–8	Spaces between individual eggs	No saturated areas
2	8–10	Few dense patches	No saturated areas
3	10–12	Many dense patches	Few saturated areas
4	12–15	Many dense patches	Moderately saturated
5	>15	Many dense patches	Many saturated areas

allowing time to observe and measure brood predation parameters. At the end of 15 min, the male was released in the vicinity of its nest. After each male was captured, the swimmer conducted assessments of the brood remaining in each nest at approximately 5-min intervals. The snorkeler recorded predation intensity (by observing the number of brood predators present and actively feeding on the brood) and size of the remaining brood as a percentage of the original brood and the time at which the male returned to its nest after release. Snorkeler observations were terminated when the male returned, when limited daylight or cold water temperatures prevented continued observation, or when at least 60 min had passed. One day following the angling and release of the male, a swimmer returned to the nest site to determine whether or not the parental male had terminated parental care behaviors and abandoned the nest and to record a 24-h post-treatment egg score.

Occurrence and timing of brood predation

Statistical analyses conducted using SPSS v.20.0 for Mac (IBM 2011) included several combinations of predictor variables hypothesized to be associated with parameters characterizing the biological and behavioral response to brood predation during an angling event. Prior to analyses, Pearson pairwise correlations were calculated for male total length, male aggression, male vigilance, predator density, initial brood size (i.e., egg score), and predation intensity to identify collinear predictor variables. Due to significant correlations among variables describing qualities of the parental male (male size, aggression, and vigilance), principle component analysis was used to reduce those three variables into a single component (hereafter, male quality) for use in subsequent analyses.

Logistic regression was used to evaluate how male quality, predator density and egg score predict whether or not predation occurred for a particular nest. Due to the small number of observations in some lakes, a Chi-Square Exact Test was used separately to evaluate the effect of lake on the occurrence of predation and later on abandonment. Cox proportional hazard regression (Cox 1972) was used to evaluate how male quality, predator density, and egg score predicted the length of time to the onset of predation in nests. Lake was used as a categorical indicator in Cox proportional hazard regression model, and Lake Opinicon was used as a reference category based on its sample size and response variable values. For both the logistic regression on occurrence of predation and for the Cox proportional hazard regression for the time to onset of predation, egg score was used as a categorical independent predictor using polynomial contrasts. Polynomial contrasts for each egg score level (1–5) were set equal to the predicted number of free swimming fry for each egg score (ES) based on the Kubacki (In Review) estimation equation below.

$$\#\ Larvae = 1157 * ES^2 - 1038 * ES$$

Although there is variation around the Kubacki estimates of free swimming fry abundance determined by egg score, Kubacki found significant differences among scoring levels for Largemouth Bass with the exception of scores 1 and 2 potentially due to underrepresentation of nests at extremely low end of egg score category 1. Two nests with egg scores of 1, therefore, were excluded from the study, reducing the sample size to 68 nests for all analyses.

Brood predator consumption rate

For each nest, an expectation of free swimming fry abundance (RS_{exp}) was determined based on initial brood size (i.e., egg score) using the Kubacki estimates described above. Periodic assessments quantifying predation were recorded at various intervals across different test nests. To facilitate comparisons among nests, estimates of percent brood remaining and predation intensity were calculated for every 5-min interval (e.g., at 5 min, 10 min, 15 min, and so on) using straight-line interpolation between adjacent, actually observed values. Estimates of the number of expected free swimming fry remaining after predation (RS_{obs}) were calculated by multiplying RS_{exp} by the percentage of the brood remaining at the last observation or when the male returned to the nest after being released. For each nest, predation intensity (P) was calculated as the mean number of predators across all observations, standardized to a per-min rate. Instantaneous consumption rates (CR_t) for each nest were based on interpolated 5-min estimates and calculated for each 5 min interval as follows:

$$CR_t = {}^{RS_{t-1} - RS_t} \Big/ \frac{P_{t-1} + P_t}{2} \Big/ 5\ \ min$$

where RS_t is the expected number of free swimming fry remaining estimated at time interval t and P_t is the predation intensity observed at the time interval. Mean consumption rate ($\overline{CR}$) for each nest was calculated as the mean of all observations of CR_t and a general linear model was used to evaluate how fixed factors (lake, egg score) and covariates (male quality, predation intensity) predict differences in mean consumption rate across nests. Lake Opinicon was used a reference category for lakes based on its sample size and response variable value, and the highest egg score value (ES=5) was used as a reference category in the general linear model. A Tukey's HSD post-hoc test was used to evaluate differences in mean consumption rates across significant predictors.

Male return and abandonment

Males that were not observed returning to the nest on the angling day were excluded from analyses of return time and abandonment. Cox proportional hazard regression was used to evaluate how lake, male quality, predator density, and egg score predict the time elapsed between release of the male and his return to the nest (hereafter "return time") on the day of the angling event. Logistic regression was used to evaluate how male quality, predator density, and change in brood size predict whether males abandoned their nests 24 h after the angling event, and a Chi-square test was used to assess the variation in abandonment rates across lakes.

Results

Male vigilance and aggression were positively correlated (r=0.36; p<0.01) while male size was negatively correlated with both aggression (r=−0.31; p=0.01) and vigilance (r=−0.35; p<0.01). Principle components analysis reduced male aggression, vigilance and male size predictors to a single component explaining 55.9 % of the variation in the data with a negative component loading for male size (−0.739) and positive loadings for vigilance (0.767) and aggression (0.744). Predator density was correlated with predation intensity (r=0.53; p<0.01), but no other predictor variables were correlated.

Predation occurred in 44 of 68 nests observed (65 %) and our analysis suggests that certain lakes had a higher proportion of nests that experienced predation (Chi-square exact test=14.699; df=8; p=0.053; Table 1). Across all lakes, predation was more likely to occur in nests belonging to smaller but more aggressive and vigilant males (i.e., higher "male quality" component score; Table 3; Fig. 1), may have been more likely in nests with higher densities of nest predators nearby (Mann–Whitney U=333.0; p<0.01). Where predation occurred the onset of predation was sooner after the removal of the male in nests with higher brood predator densities, and onset of predation varied across lakes (Table 3; Fig. 2).

Mean consumption rate ($\overline{CR}$) trended higher in nests with higher initial brood size (Table 4) but post-hoc Tukey HSD test did not identify significant pair-wise differences (Fig. 3). Likewise, mean consumption rate did not vary by male quality, predation intensity (i.e., mean number of predators in the nest) or across lakes (Table 4). Overall mean consumption rate for all nests that experienced predation was 20.9±6.5 free swimming fry eaten predator^{-1} min^{-1}, and the instantaneous consumption rate was generally greatest in the first 15 min of exposure (Fig. 4).

After being held in a live well for 15 min, the mean return time of a male was 30.0 min (95 % CI range=18.7–41.3 min), resulting in a total time of absence ranging from 33.7 to 56.3 min. Return time varied across lakes primarily due to significant differences in return time between Wolfe Lake nests and the reference lake, Lake Opinicon. Return time was not associated with variation in parental male qualities, predator density, or egg score (Table 5). Across all lakes, 15 of 48 (31 %) males with nests that experienced predation abandoned their nests after 24 h while only 3 of 24 (13 %) males with nests that experienced no predation abandoned their nest (Chi-Square=2.508; df=1; p=0.11). The probability of a male Largemouth Bass abandoning its nest after 24 h did not vary across lakes (Chi-square=2.083, df=8, p=0.09), or in relation to male quality principle component scores. Males that experienced a smaller change in brood size due to predation were less likely to abandon their nests (Table 3).

Discussion

The density of brood predators in the vicinity of a Largemouth Bass nest varies across lakes (Gravel and Cooke 2009) and is an important component of the complex behavioral dynamics that structure brood predation dynamics during a catch-and-release angling event. The onset of predation as well as predation intensity were related to the number of predators near the nest site prior to angling, indicating that populations from lakes with high densities of brood predators are at risk for more immediate onset of intense brood predation

Table 3 Summary of model results evaluating the occurrence of brood predation, the time elapsed prior to the start of consumption of eggs by a brood predator, and the occurrence of abandonment of the nest

Response variable (test) Predictor variable	exp (β)	exp (β) 95 % CI (lower–upper)	Wald's χ^2	df	p
Occurrence of brood predation (logistic)			26.55	5	<0.01*
Male quality	2.53	(1.23 – 5.18)	6.43	1	0.01*
Predator density	1.42	(0.99 – 2.03)	3.64	1	0.06
Initial brood size			4.04	3	0.26
Egg Score 2	0.55	(0.06 – 4.70)	0.30	1	0.58
Egg Score 3	5.31	(0.94 – 29.91)	3.58	1	0.06
Egg Score 4	0.60	(0.18 – 1.97)	0.71	1	0.40
Constant	1.95		2.15	1	0.14
Time to predation (Cox proportional hazard)			30.63	12	<0.01*
Male quality	1.60	(0.89 – 2.86)	2.48	1	0.12
Predator density	1.11	(1.04 – 1.19)	9.25	1	<0.01*
Initial brood size			6.01	3	0.11
Egg Score 2	1.19	(0.48 – 2.98)	0.14	1	0.71
Egg Score 3	2.31	(0.84 – 6.37)	2.61	1	0.11
Egg Score 4	0.64	(0.33 – 1.24)	1.78	1	0.18
Lake			16.54	7	0.02*
Charleston	0.98	(0.08 – 11.58)	< 0.01	1	0.99
Long	0.58	(0.08 – 4.34)	0.28	1	0.60
Loughborough	3.34	(0.97 – 11.46)	3.66	1	0.06
Maholey	0.65	(0.17 – 2.51)	0.39	1	0.53
Mills	0.21	(0.06 – 0.67)	6.98	1	0.01*
Otter	0.63	(0.07 – 6.04)	0.16	1	0.69
Whitefish	0.79	(1.84 – 3.42)	0.10	1	0.76
Occurrence of nest abandonment (logistic)			8.93	3	0.03*
Male quality	0.58	(0.31 – 1.09)	2.84	1	0.09
Predator density	1.00	(0.90 – 1.10)	0.01	1	0.93
Change in brood size	1.17	(1.01 – 1.36)	4.15	1	0.04*
Constant	0.17		16.74	1	<0.01*

*Indicates significance at alpha= 0.05

after the male is angled from the nest. Once predation began, nests with lower mating success were associated with lower consumption rates on a per-predator basis. Nests with the highest egg scores, however, had similar (but highly variable) consumption rates, indicating that brood predators reach a consumption rate limit when offered a large amount of eggs in a nest. Duration of exposure has been shown to be related to how long and under what handling conditions (e.g., air exposure, live well) the male is held by the angler (Hanson et al. 2007). Largemouth Bass held in a live well for 1 h, for example, take significantly longer to return to their nest than immediately released bass, and in the process they can lose 90 % or more of their brood, resulting in a high rate of nest abandonment (Hanson et al. 2007). Tournament caught Largemouth Bass, therefore, are highly likely to have their broods significantly reduced or eliminated before they are released and return to the nest. Largemouth Bass included in this study were held for 15 min so that the range of impacts of progressively longer hold times on brood predation dynamics could be estimated. The proportion of abandoned nests observed in this study may be atypically high if typical "immediate" catch and release angling events never approach 15 min hold times, but likely underestimate abandonment rates in tournament situations where hold times exceed several hours. Returning to the nest, however, does not guarantee survival of the remaining offspring because brood loss incurred during the male's absence is a critical factor that determines whether the male will choose to continue providing parental care or abandon its brood (Zuckerman and Suski 2013). Anglers immediately

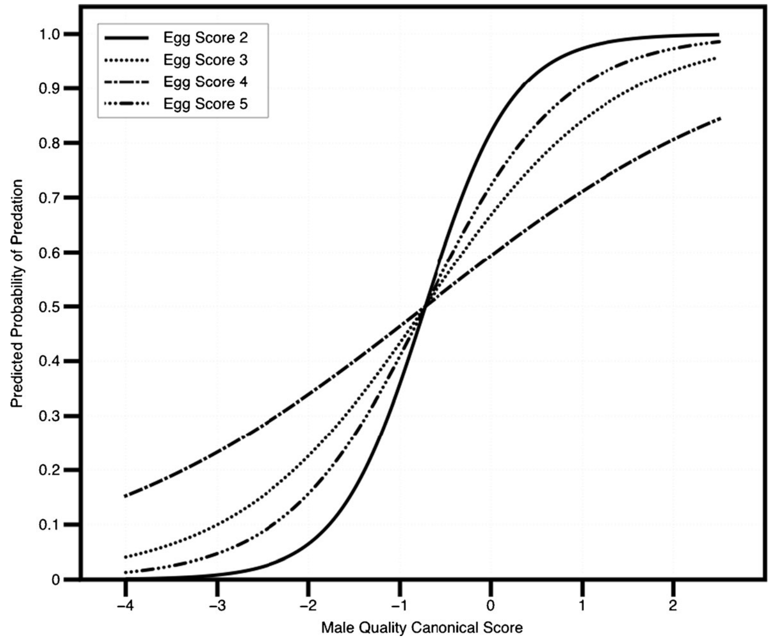

Fig. 1 Probability of predation as predicted by the logistic regression model reported in Table 3 using male quality principle components analysis canonical scores as a predictor across egg scores. Higher canonical scores indicate smaller male size with higher aggression and vigilance scores

releasing captured male nesting Largemouth Bass and practicing proper handling (Suski et al. 2004; Pelletier et al. 2007), therefore, will reduce the window of opportunity for the onset of brood predation and minimize return times, thus lowering the risk of brood reductions that trigger abandonment.

Findings in this study indicated that male size was negatively correlated with aggression and vigilance, contrary to other studies that associated male size with higher aggression, as well as reproductive success (Philipp et al. 1997; Suski and Philipp 2004). These studies, however, did not consider how nest site selection might impact predator densities near the nest, and how predator density may affect short-term aggression and vigilance behaviors. Once large, aggressive males secure a high quality nest site with fewer nest predators

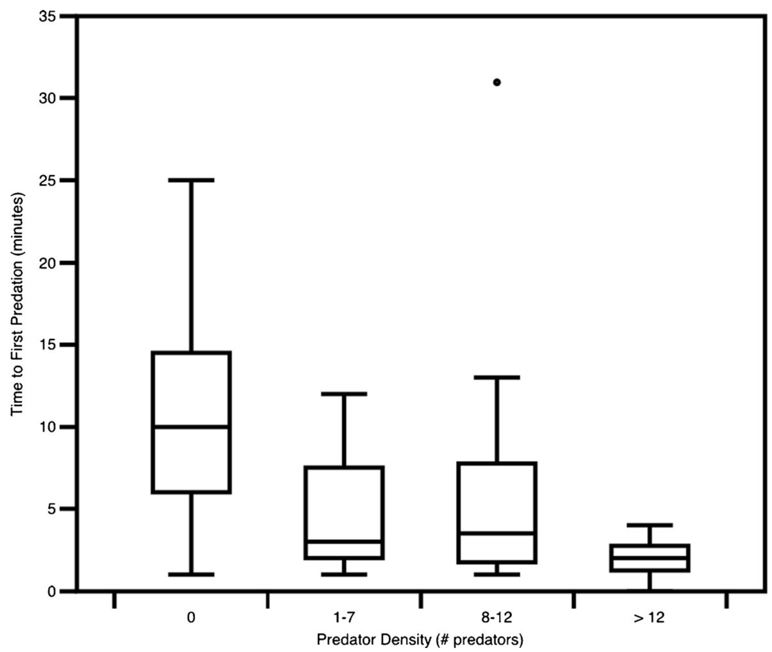

Fig. 2 Boxplot showing the time to first predation across four groups of predator densities. Predator density groups all nests with no predators near the nest prior to angling followed by the first quartile, interquartile, and third quartile of nests based on predator density. The *center line* of the boxplot represent the group mean, *box edges* represent the interquartile range, *whiskers* indicate 95 % confidence limit, and *points* represent outliers

Table 4 Summary of general linear model results evaluating the relationship between male quality, predation intensity, and initial brood size on the mean rate of consumption $\overline{CR}$ of larvae by brood predators across lakes

Predictor variable	β (SE)		95 % CI β (lower–upper)	F	df	*p*
Overall model				2.55	12	0.02*
Male quality	0.73	(4.76)	−8.98 – 10.45	0.02	1	0.88
Predation intensity	−0.51	(0.42)	−1.37 – 0.35	1.47	1	0.23
Initial brood size				3.97	3	0.02*
Egg Score 2	−29.70	(11.38)	−52.92 – −6.49	−2.61	1	0.01*
Egg Score 3	−22.74	(10.52)	−44.18 – −1.29	−2.16	1	0.04*
Egg Score 4	−4.94	(12.63)	−30.69 – 20.81	−0.39	1	0.70
Lake				1.05	7	0.42
Charleston	3.39	(23.45)	−44.44 – 51.23	1.45	1	0.89
Long	−9.39	(16.02)	−42.07 – 23.28	−0.59	1	0.56
Loughborough	3.13	(10.08)	−17.44 – 23.69	0.31	1	0.76
Maholey	22.45	(10.87)	0.28 – 44.62	2.07	1	0.05*
Mills	7.64	(9.65)	−12.05 – 27.32	0.79	1	0.44
Otter	8.57	(21.36)	−35.01 – 52.14	0.40	1	0.69
Whitefish	−2.66	(12.47)	−28.10 – 27.78	−0.21	1	0.83
Constant	37.43	(11.36)		3.30	1	<0.01*

*Indicates significance at alpha= 0.05

in its vicinity, aggressive behaviors may diminish resulting in lower aggression and vigilance scores. Smaller males may have been relegated to lower quality nests sites with higher local predator densities, causing the smaller males to be more active in nest defense behaviors, resulting in higher aggression and vigilance scores. Lakes in this study may have varied in other parameters known to affect certain aspects of black bass reproductive ecology but notable differences in, for instance, coarse woody habitat (Hunt and Annett 2002; Lawson et al. 2011), among these lakes was not apparent. Future studies should include nest site quality relative to exposure to nest predators and the importance of local predator densities on nest defense.

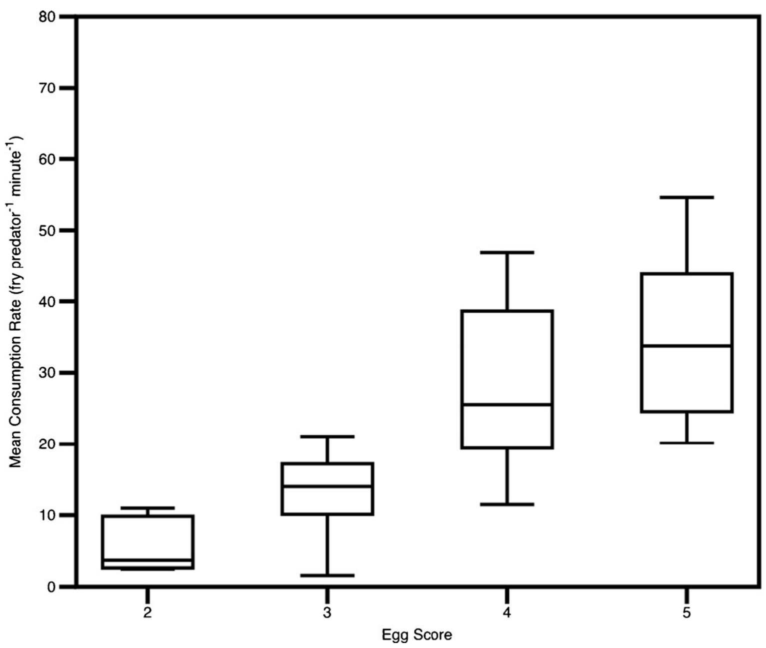

Fig. 3 Mean consumption rate (free swimming fry predator^{-1} min^{-1}) across four egg scores. *Error bars* represent 95 % confidence interval on the mean based on a t-distribution at alpha= 0.05. Post hoc Tukey HSD tests detected no significant pair-wise differences in mean consumption rate. Egg score 1 was not included in the analysis due to low sample size

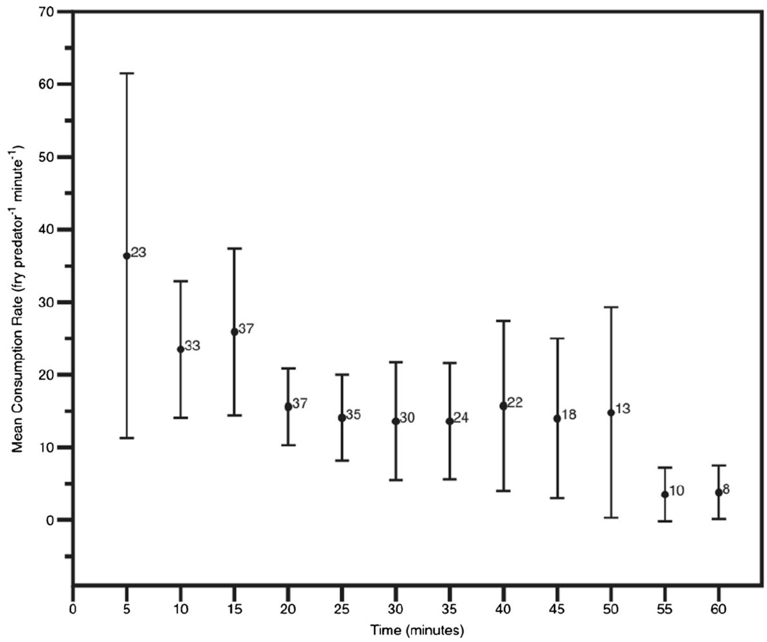

Fig. 4 Mean consumption rate (free swimming fry predator^{-1} min^{-1}) calculated for all nests on 5-min intervals. *Error bars* represent 95 % confidence interval on the mean based on a t-distribution at alpha=0.05, and labels indicate number of nests included in the calculation of the mean at each time interval

Fisheries managers must balance the goal of providing quality angling opportunities throughout the year with the need to protect spawning bass to ensure successful reproduction in the population. Managers should evaluate the level of risk associated with angling nesting bass by assessing predator densities and angler catch rates during the spring spawning season. In cases where angler catch rates and brood predator densities are high, brood predation is likely to occur quickly and have significant negative impact on brood survival; therefore leaving such a fishery open to catch-and-release angling during the spawning season likely increases risk of reproductive failures. The effectiveness of implementing immediate catch-and-release only restrictions, for

Table 5 Summary of Cox hazard regression model results evaluating the relationship between male quality, predator density, and initial brood size on the time it took males to return to their nests across lakes

Predictor variable	exp β	exp (β) 95 % CI (lower–upper)	Wald's χ^2	df	*p*
Overall model			22.44	13	0.05*
Male quality	1.02	0.65 – 1.61	0.01	1	0.92
Predator density	1.00	0.96 – 1.04	< 0.01	1	0.98
Initial brood size			0.67	3	0.88
Egg Score 2	1.26	0.51 – 3.08	0.25	1	0.61
Egg Score 3	1.25	0.52 – 2.97	0.25	1	0.62
Egg Score 4	0.91	0.53 – 1.57	0.12	1	0.73
Lake			17.05	8	0.03*
Charleston	3.03	0.57 – 16.19	1.67	1	0.20
Long	0.22	0.05 – 1.04	3.67	1	0.06
Loughborough	0.48	0.17 – 1.36	1.90	1	0.17
Maholey	1.35	0.49 – 3.77	0.34	1	0.56
Mills	1.08	0.36 – 3.26	0.02	1	0.90
Wolfe	5.44	1.23 – 23.99	5.00	1	0.03*
Otter	0.73	0.09 – 6.20	0.08	1	0.77
Whitefish	2.59	0.66 – 10.20	1.84	1	0.18

*Indicates significance at alpha= 0.05

example, will vary (e.g., Kubacki et al. 2002) in large part because the risk of brood predation varies across lakes, perhaps at larger spatial scales. Further study is needed to better understand how variations in reproductive success at the level of the population can impact recruitment dynamics in Largemouth Bass.

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