Fisheries Research 259 (2023) 106580

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

COVID-19 reduced recreational fishing effort during the black bass spawning season, resulting in increases in black bass reproductive success and annual recruitment

David P. Philipp[a,*], Aaron Zolderdo[b,c], Michael J. Lawrence[d], Julie E. Claussen[a], Liane Nowell[e], Peter Holder[c], Steven J. Cooke[a,c]

[a] *Fisheries Conservation Foundation, 302 E. Green Street #2102, Champaign, IL 61820, USA*
[b] *Queen's University Biological Station, 280 Queen's University Road, Elgin, ON K0G 1E0, Canada*
[c] *Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada*
[d] *Department of Biological Sciences, University of Manitoba, Sifton Road, Winnipeg, MB R3T 2N2, Canada*
[e] *Kenauk Institute, 1000 Chemin Kenauk, Montebello, QC J0V 1L0, Canada*

A R T I C L E I N F O

Keywords:
Angling nesting bass
Reproductive success
Annual recruitment, bass spawning. sanctuaries
COVID

A B S T R A C T

In Opinicon Lake, Ontario during two non-pandemic years (2019 and 2022) the hook-wounding rates from recreational angling observed among nesting male largemouth bass *Micropterus salmoides* (LMB), and nesting male smallmouth bass *Micropterus dolomieu* (SMB), were quite high, but typical of those observed in the lake over the last 20 years of monitoring. That level of illegal, preseason angling resulted in very low percentages of both LMB and SMB nesting males being successful at raising their broods to independence, rates comparable to those observed for this lake in previous years. In 2020 and 2021, amid the COVID-19 pandemic, however, access to fishing in Ontario was severely limited during the bass spawning season, which serendipitously provided a natural "whole-lake bass spawning sanctuary" to study. Not surprisingly, the hook-wounding rates for nesting male LMB and SMB in Opinicon Lake were the lowest rates ever observed over the last 30 + years. Concomitantly, the percentage of nesting male LMB and SMB that were successful at raising their broods to independence was approximately 3–4 times greater than that in the non-COVID years. Not unexpectedly, those increases in nesting success translated to similar increases in LMB and SMB reproductive success (production of post parental care, independent fry). More importantly, those increases further resulted in large increases in the annual recruitment of both LMB and SMB. This unanticipated COVID-driven experiment revealed that using bass spawning sanctuaries would be more efficient than closed seasons as a management strategy to conserve levels of black bass annual recruitment.

1. Introduction

Largemouth bass (*Micropterus salmoides*; LMB) and smallmouth bass (*M. dolomieu*; SMB), are two species of black bass native to much of eastern North America, including our study sites in southern Ontario (Scott and Crossman, 1973; MacCrimmon, Robbins, 1975). These species arguably serve as the basis for the most economically important sport fishery in North America, one valued in the billions of US$ annually (Quinn, 2002; Quinn and Paukert, 2009). Developing sound, science-based strategies to responsibly and sustainably manage and conserve these valuable natural resources well into the future, therefore, makes sense from both an environmental and an economic standpoint. The complex life history for these two species, however, complicates developing effective management and conservation strategies. That is, males of both species are entirely responsible for building nests, courting females for spawning, and then solely providing extended parental care of the resulting offspring for another 4–6 weeks post fertilization. Uninterrupted parental care during development is imperative for offspring survival (Ridgway et al., 1989; Gross and Kapuscinski, 1997; Philipp et al., 1997; Gross, 2005; Cooke et al., 2006; Barthel et al., 2008; Parkos et al., 2011). If a male abandons (or is removed from) his nest during this parental care period, brood predators will quickly consume all of the offspring (Suski et al., 2003; Zuckerman et al., 2014), with upwards of 50% being preyed upon within the first 8–10 min of the male's absence

* Corresponding author.
E-mail address: philipp@illinois.edu (D.P. Philipp).

https://doi.org/10.1016/j.fishres.2022.106580
Received 23 February 2022; Received in revised form 1 December 2022; Accepted 2 December 2022
Available online 6 December 2022

(Stein and Philipp, 2015). In situations where anglers catch and harvest nesting bass, rapid predation of the entire brood occurs universally.

Catch-and-release angling, however, can theoretically allow an angled nesting male the opportunity to return to his nest and resume guarding his brood. Whether a post-release male does in fact resume his parental care or abandons the brood, however, depends on several factors, including the size (fitness value) of the brood, the handling of the fish by the angler during the catch-and-release process, and the condition of the male before and after the angling event (Philipp et al., 1997; Cooke et al., 2000; Suski et al., 2002, 2003; Suski and Philipp, 2004; Hanson et al., 2007; Steinhart et al., 2008; Zuckerman et al., 2014). Decades ago, the Ontario Ministry of Natural Resources instituted in many areas across the province a seasonal closure of fishing for nesting black bass during the spawning season to protect black bass reproductive success. Currently, for Opinicon Lake and many of the other popular black bass fishing regions in the province that closed season is defined as the period from December 15th until the third Saturday in June. That regulation specifically prohibits the use of angling tactics that would hook nesting male bass (Kubacki et al., 2002). The fact that it is legal during this period to fish for other species such as northern pike (*Esox lucius*), walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), various salmonid species, and all centrarchid species other than black bass (*Micropterus spp*), however, complicates compliance with and enforcement of that regulation. There is often substantial overlap in habitat use between these legally accessible species of fishes and nesting black bass, which can cause the inadvertent capture of nest-guarding black bass by well-intentioned anglers. Unfortunately, some anglers use this "loophole" in the regulation to (illegally) target, catch, and release nesting male bass, thereby rendering this regulation ineffective at accomplishing its objective of protecting black bass reproductive success and recruitment (Philipp et al., 1997; Quinn, 2002; Kubacki et al., 2002; Suski et al., 2002; Steinhart et al., 2008; Zuckerman et al., 2014).

The negative impacts of angling (even catch-and-release) on the nesting success (i.e., whether or not a male was successful in raising his brood to independence) and reproductive success (the number of independent post-parental care fry produced) of individual male black bass is well documented (Philipp et al., 1997; Cooke et al., 2000; Suski et al., 2002, 2003; Suski and Philipp, 2004; Steinhart et al., 2004, 2008; Hanson et al., 2007; Diana et al., 2012; Zuckerman et al., 2014; Twardek et al., 2017). Some authors, however, have questioned whether or not there is a population-wide negative impact on annual recruitment from such angling of male nesters (e.g., Jackson et al., 2015, Trippel et al., 2017).

It is also well-accepted that a wide range of both biotic (e.g., adult abundance and condition, larval prey availability, switch to piscivorous diets, vegetation coverage, etc.) and abiotic (e.g., weather, water temperature and quality, turbidity, etc.) factors can affect successful reproduction and recruitment among all fish (Cushing et al., 1996) including black bass. Traditional dogma assumes that annual recruitment among black bass populations is determined primarily by some combination of those environmental factors, and that any underproduction (or overproduction) of offspring is muted by some density-dependent compensation mechanism. Inherently, this thinking presumes that there is no positive relationship between lake-wide reproductive success and annual recruitment. Furthermore, this thinking also predicts that as angling pressure increases on nesting male black bass, overall recruitment remains unaffected (Jackson et al., 2015; Trippel et al., 2017), and, therefore, that angling nesting male bass should not represent a major concern for managers.

Our working hypothesis differs from that traditional dogma, stating instead that although black bass reproduction and recruitment are indeed affected by environmental variables, any reduction in reproductive success results in reduced annual recruitment as well. Our hypothesis proposes that there is a strong positive relationship between reproductive success and annual recruitment, and that as angling pressure increases on nesting male black bass, recruitment will be reduced

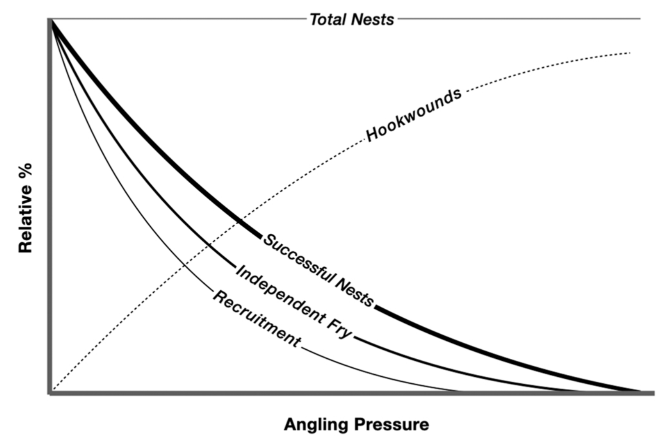

Fig. 1. A conceptual model of the relationship between reproductive metrics and recruitment and the impacts that angling has on them.

(see Fig. 1). To be clear, however, under our hypothesis, in any given lake the magnitude of that negative impact would depend upon the level of angling pressure exerted on the nesting male population. Large lakes with lots of cover, good spawning substrate, low water clarity and an abundant bass population might not be substantially affected by a low to moderate level of angling pressure during the spawning season. Alternatively, smaller lakes that are exceptionally clear and free of aquatic vegetation, allowing anglers to not only find nests easily, but also to see the male bass guarding them, could have their nesting/reproductive success reduced substantially by extensive angling (even catch-and-release angling) and as a result, their annual recruitment reduced significantly as well.

The current fishing regulations in much of eastern Ontario, which include seasonal angling closures for black bass, appear to be insufficient to provide long-term protection for local black bass populations. The high level of non-compliance coupled with the lack of enforceability (Philipp et al., 1997; Quinn, 2002; Kubacki et al., 2002; Suski et al., 2002) in Opinicon Lake, for example, result in the current regulation failing to fully protect any nest-guarding black bass from incidental or illegally targeted fishing. As a result, we have proposed (Kubacki et al., 2002; Suski et al., 2002) replacing the current seasonal closure strategy with a system of bass spawning sanctuaries, i.e., areas where bass fishing is closed to all angling, but only for the duration of the black bass reproductive period. Such a regulation would be clearly enforceable; any angling whatsoever within the bass spawning sanctuary would be considered illegal. Based on our past assessments of bass reproduction within Opinicon Lake over the last 30 + years, including three different years in which our team swam and mapped all black bass nests along the entire shoreline of Opinicon Lake, we speculate that by designating the right 30% of the lake's shoreline areas as bass spawning sanctuaries, upwards of 70% of all nesting black bass in the lake could be protected from angling. The efficacy of implementing such seasonal angling sanctuaries/no fishing areas in protecting bass reproductive success and recruitment, however, has not yet been tested to any great extent.

To address that issue, we launched a pilot study in 2019 to test the efficacy of seasonal bass spawning sanctuaries. Opinicon Lake was chosen as the site for this pilot study because of the extensive information that has been gathered in this lake over the past few decades on black bass and other sunfish nesting biology (e.g., Keast et al., 1978; Philipp et al., 1997; Gross, 2005; Gravel and Cooke, 2009; Zolderdo et al., 2016, 2019), as well as our previous experience on the lake. For this pilot study, we selected five areas within Opinicon Lake that had previously been identified as having excellent bass spawning habitats for largemouth and/or smallmouth bass. These areas were chosen to encompass both potential spawning sanctuaries and non-sanctuary controls and were based upon previous snorkeling assessments of lake-wide black bass spawning activity. The original plan was to gather baseline data on mating, nesting, and reproductive success of largemouth and smallmouth bass in these five areas over three years prior to establishing the experimental spawning sanctuaries, thereby having them serve as baseline, pre-treatment controls in a BACI design experiment. In 2019, we began this observational study and planned on continuing that data gathering activity in 2020 and 2021. During the spring of 2020, however, the rapid global spread of COVID-19 resulted in the closure of all but essential services in Ontario, which was accompanied by substantial reductions in travel and tourist activities (Gössling et al., 2020; Lemieux et al., 2020; Rutz et al., 2020; Ontario OFAH, 2020; Howarth et al., 2021). During this time, fishing in many areas of Ontario was severely limited by either partial or complete restriction of access to many local parks, conservation areas, boat launches, marinas, and access points (see OFAH, 2020, Paradis et al., In Press). While angling effort and catch rates during the COVID-19 pandemic have yet to be quantified across the province via forthcoming studies that will rely on anglers reporting their activities via smartphone apps, it is widely accepted that fishing pressures were greatly reduced during this bass nesting timeframe across much of Ontario (i.e., early May – early July in most inland lakes), and certainly in Opinicon Lake. Opinicon Lake is frequented by American tourists who were restricted from entering Canada until August of 2021 because of COVID rules. The combination of these unusual and unanticipated circumstances eliminated the use of 2020 (and 2021) as any kind of "normal" year for assessing the impacts of illegal preseason angling on bass reproduction. Instead, it serendipitously provided us with an unintentional "whole-lake sanctuary" experiment that we have used to reveal the potential benefits of using seasonal bass spawning sanctuaries as a management strategy for increasing successful black bass reproductive success and annual recruitment. The fortuitous timing also allowed us to provide early information detailing how COVID-19 may have impacted fish recruitment patterns in Ontario.

2. Methods

2.1. Study site

This study was conducted in Opinicon Lake, Ontario (Fig. 1 44°33'33.3"N 76°19'49.3"W), which is a 780-ha mesotrophic lake with a mean depth of 4.9 m and a maximum depth of 9.2 m (Agbeti et al., 1997). Opinicon Lake is part of the Rideau Waterway system and is in the Cataraqui River watershed. Black bass reproduction (both LMB and SMB) was monitored along five shoreline transects that varied from 700 to 1100 m in total length during the spawning seasons of 2019 – 2022 (i.e., before, during, and after the COVID-19 pandemic restrictions). These sites had been identified during previous lake-wide surveys of the entire shoreline as areas representative of the lake as a whole, and where black bass nested in moderate-high density each year. These sites were also projected to be part of a study of bass spawning sanctuaries to be conducted over the following few years as pre-treatment years to gather baseline data for both sanctuary and control sites. The change in fishing pressure caused by the onset of the COVID-19 pandemic, however, canceled those plans, but provided the serendipitous opportunity described herein.

2.2. Bass reproductive surveys

Spring snorkel surveys using previously described survey techniques (e.g., Philipp et al., 1997; Siepker et al., 2006; Dey et al., 2010; Zolderdo et al., 2016) were used to assess the mating success, nesting success, and reproductive success of both LMB and SMB, as well as the level of hook-wounding observed on nesting males of both species. For this, snorkelers swam the littoral zone along the five study transects every 3–6 days from the beginning of black bass spawning in early-mid May until the end of parental care, when the black bass offspring reach independence, a developmental stage that includes active foraging behaviors as well as the capability to recognize and avoid predators (Brown, 1984, 1985). The parental care period for successful LMB and SMB usually lasts 4–6 weeks post-spawning (Ridgway et al., 1989; Cooke et al., 2002). During each snorkel survey, black bass nest locations were recorded on a detailed map of the area, with each nest being assessed for nest depth, male total length, mating success (i.e., number of eggs), the developmental stage of the brood (used to back calculate the spawn date), and the presence and location of any hook wounds on the parental male (Philipp et al., 1997, Suski et al., 2004). During subsequent surveys, snorkelers documented the presence/absence of the guarding parental male, identified the developmental stage of the brood (Philipp et al., 1985), confirmed the assessment of mating success, and assessed the presence of any hook wounds on the male. The length of the egg-laying period (i.e., the number of days from when the first eggs were spawned in bass nests until the last were spawned, regardless of whether those nests were successful or not) was determined for each species for each year of the study. Multiple hook wounds were assessed by recording the date and location of every hook wound observed on the bass' mouth during each snorkel survey. In this way, the entire developmental history of each brood and the hook-wounding history of each male were followed throughout the parental care period provided by its guarding male.

2.3. Determining mating success and nesting success

For each nest with a parental male present guarding a brood, snorkelers visually assessed its mating success (i.e., its egg score, which equals the number of eggs spawned in each nest) and assigned it a score of 1–5 (Table 1), as defined previously (Stein and Philipp, 2015). Nesting was determined to be successful if the parental male remained guarding its brood until the brood reached the independent fry stage or as unsuccessful if the male abandoned (or was removed from) its brood, which was then rapidly consumed by predators (Philipp et al., 1997; Stein and Philipp, 2015). For SMB males that remain at the nest site with their offspring for all of parental care, the nest was determined to be successful when the fry had metamorphosed from the solid black stage to become green/brown pigmented with vertical dark bars. For LMB

Table 1
Characteristics that distinguish each level of the egg scoring system used in the current study. Diameter is an indication of the overall spread of eggs in a nest, patchiness describes the extent to which eggs are clumped together (horizontal clustering), and saturation describes the extent to which eggs have been deposited on top of each other (vertical clustering).

Largemouth Bass Micropterus salmoides (LMB)			
Egg Score	Diameter (in)	Patchiness	Saturation
1	6–10	Spaces between individual eggs	No saturated areas
2	10–12	Few dense patches	No saturated areas
3	12–15	Some dense patches	Few saturated areas
4	151–18	Many dense patches	Some saturated areas
5	> 18	Many dense patches	Many saturated areas
Smallmouth Bass *Micropterus dolomieu* (SMB)			
Egg Score	Diameter (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	Some dense patches	Few saturated areas
4	12–15	Many dense patches	Some saturated areas
5	> 15	Many dense patches	Many saturated areas

males that move away with their brood from the actual nest site during parental care, the nest was categorized as successful when the male moved its brood of free-swimming fry more than 5 m from the nest.

2.4. Converting individual mating success (egg score) to individual reproductive success (number of independent fry)

To convert individual mating success (egg score) to an estimate of individual reproductive success (number of independent fry), a conversion equation was developed separately for SMB and LMB as previously reported (Stein and Philipp, 2015). Specifically, snorkelers located active SMB and LMB nests with each egg score of 1–5. Snorkelers then monitored each nest until the embryos developed into newly free-swimming fry (FSF), when they were easily observed swimming immediately above the nest area in a tight school of small fry guarded by the male. At this point in brood development, snorkelers used a Fubaeli fry net to collect all the fry in the brood. The Fubaeli fry net was a triangular landing net that had been modified by replacing the standard netting material with 0.5 mm mesh Nytex screen and replacing the bottom of the net material with a polystyrene powder funnel (150 mm diameter at the top) using silicone sealant. A 1 L polystyrene solution bottle was affixed to the narrow end of the funnel via compression fit, and the bottle was modified by cutting sections out of the side of the bottle and replacing them with Nytex screen to permit water drainage while capturing the FSF. A triangular frame was chosen for the net to maximize capture efficiency when sweeping the net near the surface of the substrate. To collect fry from each nest, a snorkeler made a series of slow, sweeping passes with the net in a figure eight pattern immediately above the nest substrate to herd individuals into tight groups for easy capture. Once the FSF were contained within the net, the net was slowly raised and the rim held above the surface while keeping the mesh submerged to protect captured offspring, and the side of the net washed down with lake water to concentrate larvae in the collection bottle (similar to methods used with a plankton net). The collection bottle was then removed from the net, and all FSF were decanted into a graduated cylinder. Second and third passes over the nest with the net were performed, at which point no fry were observed remaining above the nest. The collected FSF were allowed to settle to the bottom of the cylinder (15–30 s), and the volumetric measurement of the entire brood was recorded in ml. The total number of FSF in each brood was enumerated by converting the volume of settled fry into absolute numbers by counting the number of FSF in three 10 ml aliquots of settled FSF, thereby determining the average number of FSF per settled ml volume. The entire brood of FSF was then released back into the lake just above their nest, at which time they resumed swimming, and the parental males resumed guarding them. FSF counts were conducted on all of the 58 test SMB nests (9–13 nests for each egg score of 1–5) and all of the 62 test LMB nests (10–14 nests for each egg score of 1–5). The average fry count (+/- SD) for each egg score was determined as the mean of the counts from all experimentally sampled nests with that egg score (Table 2). To be clear, none of the nests that were part of the reproductive success/recruitment study were used to calculate the average FSF numbers per egg score.

2.5. Determining population-wide reproductive success

The mating success (egg score) for each successful male bass was converted to that male's individual reproductive success (RS, the number of expected independent FSF produced by successful nests) using the conversion factors shown in Table 2 and the methodology described previously (Stein and Philipp, 2015). The population-wide reproductive success (the total number of independent fry produced across all successful nests in the study site, i.e., across all five transects) was calculated for LMB and SMB separately by summing the individual RS values determined for each of the successful nests for each species across all five transects.

Table 2
Mean number of free-swimming fry (FSF) (± standard deviation and standard error, with 95% confidence limits) produced in experimentally sampled successful Smallmouth Bass (SMB) and Largemouth Bass (LMB) nests of each egg score 1–5.

Largemouth Bass *Micropterus salmoides* (LMB)			
Egg Score	**N**	Mean Fry	**SD**
1	12	890	210
2	13	2410	360
3	14	7950	670
4	13	12,800	1520
5	10	24,800	3550
Smallmouth Bass *Micropterus dolomieu* (SMB)			
Egg Score	**N**	Mean Fry	**SD**
1	12	330	111
2	13	760	215
3	11	1320	209
4	13	1940	335
5	9	2720	462

2.6. Assessing annual recruitment

Relative levels of annual recruitment for LMB and SMB were assessed independently for each spawning year using two different age metrics, young-of-the year (YOY) and one-year old juveniles (1 +). For this, we conducted a second set of snorkel surveys each year, later in the summer (late July through late September), well after all parental care activities by male bass for that year were completed and adults had moved away from the nests. For this determination, snorkelers swam the entire shoreline of each of the five transects in Opinicon Lake and visually counted the number of YOY (40–50 mm TL size class) and 1-yr old (80–120 mm TL size class) juvenile LMB and SMB observed during that survey. A total of 4–8 of these visual assessments was conducted by multiple swimmers on at least three different days each year during the late July-late September period. In this manner, the relative annual recruitment level for each year class of LMB and SMB (2019–2022) was determined in two ways. The first was as the average number of YOY (observed during the late summer snorkel surveys conducted in the same year as that year class). The second was as the average number of 1-yr old juveniles (observed during the late summer snorkel surveys conducted in the year after that year class. For example, the relative recruitment of 1 + juveniles for the 2019-year class (those fish spawned in the spring of 2019) was determined from the snorkel surveys conducted during the summer of 2020.

2.7. Data analysis

Statistical analyses were conducted in JMP (v 16.1; SAS Inc, Cary, NC). For both species, differences in hook wounds and nest success rates between COVID and non-COVID years were assessed using a chi-square test. For the remaining parameters, a paired t-test was used to detect differences between COVID (2020 and 2021) and non-COVID (2019 and 2022) years for length of the egg-laying period, total number of nests, total number of free-swimming fry (FSF), relative recruitment measured as YOY bass, and relative recruitment measured as 1 + bass. Using a strength of evidence approach for interpreting p values, $p < 0.01$ = 'strong support', $p < 0.05$ = 'moderate support', $p < 0.1$ = 'weak support', $p > 0.1$ = 'no support'. Unless otherwise stated, all values are presented as mean ± sd.

3. Results

The following is a summary of the reproductive metrics measured for SMB and LMB in Opinicon Lake in the years just before and after the COVID-19 pandemic (2019 and 2022) and in the two years during the pandemic (2020 and 2021; see Table 3). First, the mean length of the egg-laying period was greater (but not significantly so) in the non-COVID years (2019 and 2022) than in the COVID years (2020 and 2021) for both LMB (20 +/- 2.8 days vs 13.5 +/- 3.5 days; $p = 0.18$) and SMB (19 +/- 2.8 days vs 12 +/- 4.2 days; $p = 0.19$). A difference in the total number of nests receiving at least some eggs during the non-COVID years vs during the COVID years was weakly supported for LMB (110 +/- 11.3 nests vs 86 +/- 5.7 nests; $p = 0.09$) and strongly supported for SMB (53 +/- 0.7 nests vs 30 +/- 0.7 nests; $p = <0.001$). Even though there were more nests in the non-COVID years than in the COVID years, the reverse was true for the percentage (and absolute number) of male LMB and male SMB that successfully raised broods to independence, 66% vs 18% for LMB (chi-square = 43.2, $p < 0.0001$) and 72% vs 24% for SMB (chi- square = 12.4, $p < 0.0001$).

Furthermore, after converting the individual egg scores into numbers of surviving FSF across all successful broods, even though there were fewer total nests and fertilized eggs spawned during the COVID years than in the non-COVID years, there was statistically weak support for there being more surviving FSF produced for both LMB (425,000 +/- 16 vs 184,000 +/- 85; $p = 0.059$) and SMB (36,900 +/- 4030 vs 15,700 +/- 7280; $p = 0.069$), respectively (Table 3). Most importantly, that difference in reproductive success between COVID and non-COVID years translated into an even greater difference in the annual recruitment (year class strength). There was moderate to strong support for relative recruitment values (Table 3) during the COVID years being greater than during the non-COVID years, using both the YOY metric for LMB ($p = 0.019$) and for SMB ($p = 0.050$) and the 1 + juvenile metric for LMB ($p = 0.0012$) and for SMB ($p = 0.036$).

To relate the reproductive metrics to angling pressure on nesting males, we directly assessed angling activity on nesting bass within our study sites using the observed hook-wounding rates for the nesting bass guarding their broods. Those rates were substantially lower during the COVID years; 5% vs 56.5% of the nesting LMB (chi-square = 58.958, $p < 0.0001$) and 12% vs 73% of the nesting SMB (chi-square = 23.791, $p < 0.0001$), respectively, had hook-wounds (Table 3).

4. Discussion

At the outset, we stated that our working hypothesis proposes that black bass (LMB and SMB) annual recruitment is directly dependent upon their population level reproductive success, and as a result, brood losses caused by angling-induced disruption of the parental care provided to offspring by their nesting parental males results in decreased annual recruitment. Furthermore, that hypothesis predicts that there should be an inverse relationship between angling pressure and both reproductive success and annual recruitment in black bass populations. That hypothesis and its predictions are graphically illustrated in Fig. 1, and the results from our study support that hypothesis. In concordance with our predicted effect, in Opinicon Lake compared to non-COVID years (2019 and 2022), the lower level of pre-season angling pressure put on nest-guarding male bass that we observed during the COVID years (2020 and 2021) resulted in their having lower rates of abandonment and as a result, higher levels of reproductive success and annual recruitment for both LMB and SMB. The longer egg laying periods during the non-COVID years was likely due to the much greater numbers of males re-nesting after abandoning their nests in response to being angled, a phenomenon that we have observed commonly over the years. Unfortunately, very few of those re-nesting/late-spawning males successfully raise broods.

The negative impacts on the reproductive success of an individual male black bass resulting from being angled off its nest have been documented repeatedly (Philipp et al., 1997; Cooke et al., 2000; Suski et al., 2003; Suski and Philipp, 2004; Hanson et al., 2007; Zuckerman et al., 2014; Philipp et al., 2015; Stein and Philipp, 2015; Trippel et al., 2017). Several authors have questioned, however, whether or not the cumulative negative impacts on individual black bass reproductive success have any impact on population-wide annual recruitment (Jackson et al., 2015; Trippel et al., 2017). Impacting that thinking is that the evidence often cited as suggesting that angling nesting bass has no negative impacts on annual recruitment has often been mischaracterized or overstated. For example, Zipkin et al. (2008) is often cited as evidence that angling does not impact recruitment, even though that was not the conclusion or even the point of that study. In that study, which involved no angling treatment, either during or after nesting, and no measurement of any reproductive behaviors or success metrics, the authors actually assessed how the removal over seven years of an unknown but likely quite substantial amount of the (non-native, introduced) adult smallmouth bass in a small lake impacted the community structure of fish in that lake. That experimental scenario (i.e., a huge reduction in predators of young SMB) does not at all mimic assessing the impact of angling for nesting bass on reproductive success and recruitment, a scenario in which the number of predators does not change, but reproductive success does.

Perhaps more pointedly, our working hypothesis and the results of this study disagree with the conclusions of Jackson et al. (2015) for largemouth and smallmouth bass in New York, a region climatically similar to Ontario. These authors suggested that because there was no published evidence for a stock-recruitment relationship within black bass populations (i.e., no direct positive relationship between the biomass or the number of adults in a bass population and the level of annual recruitment in that population), angling nesting males should have little to no effect on annual black bass recruitment (Jackson et al., 2015). In reality a stock-recruitment relationship within populations of these species should not even be expected for the following reasons, all of which are based upon components of black bass life history. First, in all black bass populations only a percentage of mature adults actually

Table 3
Reproductive metrics of Largemouth Bass *Micropterus salmoides* (LMB) and Smallmouth Bass *Micropterus dolomieu* (SMB) in Opinicon Lake during 2019 and 2022 (pre and post COVID-19) as well as 2020 and 2021 (during COVID-19). The # Days Spawning indicates the duration of the egg-laying period. The # FSF Produced indicates the number of independent free-swimming fry produced in all of the successful nests, calculated form the observed egg/fry scores. Relative recruitment is the average of multiple snorkel surveys swims on separate days, summed across all five transects in each of the study years. Relative recruitment was assessed at two stages, as young-of-the year YOY (during their first summer of life) and as 1 + age individuals (during their second summer). The 1 + relative recruitment values, however, cannot be determined until the late summer of 2023, so are labeled as TBD.

SPECIES	*YEAR CLASS*	*# DAYS SPAWNING*	*# NESTS BUILT*	*# NESTS SUCESSFUL*	*% NESTS SUCESSFUL*	*# FSF PRODUCED*	% HOOK WOUND	YOY RELATIVE RECRUITMENT	1 + RELATIVE RECRUITMENT
LMB	2019	22	102	17	17%	124,000	61%	8.8 + /- 3.1	12.0 + /- 1.4
LMB	2020	11	78	59	76%	414,000	5%	40.5 + /- 2.1	86.3 + /- 11.2
LMB	2021	16	86	48	56%	436,000	5%	50.5 + /- 11.1	61.7 + /- 24.9
LMB	2022	18	118	22	19%	244,000	52%	10.2 + /- 4.5	TBD in 2023
SMB	2019	21	52	15	29%	20,800	69%	5.0 + /- 1.4	4.5 + /- 0.7
SMB	2020	9	30	23	77%	34,100	13%	43.8 + /- 6.1	49.8 + /- 7.8
SMB	2021	15	29	19	66%	39,800	10%	20.5 + /- 2.1	31.0 + /- 14.4
SMB	2022	17	53	10	19%	10,500	77%	7.1 + /- 4.0	TBD in 2023

attempt to spawn, and that percentage (for both males and females) can vary greatly among years even within a single population (Raffetto et al., 1990), potentially ranging from a low of 0% to a high of 100% at the extremes. As a result, the number of zygotes produced in a population can differ widely among years, even when the number of mature adults in that population is the same. Second, the percentage of nests (broods) that are abandoned by nest-guarding males before their broods have reached independence also varies from year to year depending upon a suite of (non-angling) factors that vary annually as well, including the density of brood predators, the amount of aquatic vegetation coverage, the physiological condition of the parental males, the mating success of the males (i.e., the number of eggs spawned in the nest), and weather events such as cold air temperatures and high winds (Philipp et al., 1997; Robillard, Fox, 2006; Steinhart et al., 2006, 2008; Gravel and Cooke, 2009; Zuckerman et al., 2014). Hypothetically then, for two years in which the same number of zygotes were produced, the percentage of those zygotes that survive to become fry that were independent of their parental male (and only then capable of survival on their own) could differ substantially as well. As a result, even without the impact of any human activities, including recreational angling, no discernable stock-recruitment relationship should be expected for any black bass population. Our working hypothesis, however, instead states that annual recruitment in black bass populations is determined by the level of reproductive success, not the number of adults, and that is a very different proposition.

In their publication Jackson et al. (2015) use data from three lakes in the State of New York (two of which, Erie and Oneida are by far the largest lakes in NY) to suggest that a relaxation in statewide fishing regulations allowing catch-and-release angling for nesting bass has had no negative effects on annual recruitment levels. Instead, the authors argued bass recruitment levels are determined by random environmental factors, perhaps being bolstered through some form of compensation (Jackson et al., 2015). That study, however, was simply a comparison of black bass year class strength in Lake Erie and two other large lakes in NY in years before and after a new statewide catch-and-release regulation went into effect. Several problems with the experimental design render the results irrelevant to assessing the impact that angling nesting black bass has on their annual recruitment. First, in the Lake Erie component of the study there was no assessment of actual angling pressure on nesting black bass (i.e., during the spring nesting period) before or after the regulation changed, nullifying the assumption that the new regulation actually caused a difference in angling pressure on nesting bass. Experience with the lack of compliance with a closed season for bass angling in Ontario suggests that the change in the regulation may not have actually increased the number of fishers angling bass off nests, but rather just made those that did previously now legal. Second, because of the seasonal patterns of the water temperatures in Lake Erie, most smallmouth bass spawning areas do not reach the 12–14 C minimums for bass to initiate nesting/spawning activities until well into June. Extraordinarily few if any, smallmouth bass males would have raised successful broods by the end of the new catch-and-release season (Kubacki et al., 2002). The new catch-and-release/no harvest seasonal regulation that was instituted statewide in New York (i.e., no harvest until the third Saturday in June) continues to be ineffective in protecting nesting smallmouth bass in the colder waters of Lake Erie. Together, these two issues combine to suggest that the amount of pre-season catch-and-release angling for nesting bass in Lake Erie (and Oneida and Canadarago as well) may not have changed following the institution of the catch-and-release regulation. Finally, the Lake Erie ecosystem has undergone some extensive changes since 1981, owing to changes in human behaviors, angling activity, introduced species, and environmental regulations. In light of these issues, we believe that drawing any conclusions on how the new regulation impacted black bass populations across New York (and other areas) based on that report is unjustified.

4.1. Management implications

This once-in-a-lifetime experiment caused by the global pandemic provided a unique opportunity that has helped develop the rationale for challenging current bass management strategies and testing new approaches (Cooke et al., 2021). COVID-19 and the associated lockdowns in 2020 and 2021 resulted in major disruptions in human behavior that impacted fishing and fish populations (e.g., Pinder et al., 2020; Midway et al., 2021). Furthermore, it provided a serendipitous experiment that demonstrated two things. First, our results documented that angling nesting bass resulted in a decrease in population-wide reproductive success that translated into a decrease in population-wide annual recruitment. Second, they showed that black bass reproductive success and recruitment could be protected by eliminating angling pressure during their reproductive period. Consequently, in regions where nest guarding species (e.g., any of the black basses), are actively managed, future management approaches should assess the efficacy of spawning sanctuaries to maintain recruitment in local populations rather than rely on a species-by-species closed season approach.

We do, however, want to acknowledge that our past research studies on LMB and SMB have been located in northern climates, mostly in Ontario, Quebec, and Illinois, where the duration of the spawning season is short. As such, we do not know how closely our hypothesis translates to other black bass species in more southerly climates. For example, the Florida bass *M. floridanus* has a spawning season that can last as long as six months (Waters and Noble, 2004; Gwinn and Allen, 2010; Trippel et al., 2017), whereas the duration of the spawning season for LMB and SMB in Opinicon Lake is typically less than 2–3 weeks. That extended spawning season exhibited by Florida bass (Shaw, Allen, 2016; Trippel et al., 2017) allows for males to renest multiple times within a single season and could complicate the relationship between reproductive success and recruitment, even blurring the definition of year class. Shaw, Allen, 2016, however, did find evidence in Florida bass for a relationship between the number of successful nests and recruit density even after only four years of study. Furthermore, although Trippel et al., 2017 reported that experimental angling of nesting Florida bass in artificial experimental 1-acre ponds had no impact on recruitment, the limitations of the experimental design in that two-year study coupled with the vagaries of conducting that type of production experiment in a few small ponds renders the conclusions equivocal. As a result, the hypothesis that the population level impact of angling nesting bass varies latitudinally or across different species of *Micropterus* is interesting, but untested. Clearly, more extensive characterizations of angling pressure-recruitment relationships are needed across systems, species, and environmental contexts. In any case, it is time for anglers and fisheries management agencies to reassess how their angling may be adversely affecting bass populations and change behaviors appropriately. One such area that stands out as an excellent starting point for such an assessment are tournaments conducted during the bass reproductive period.

CRediT authorship contribution statement

David P. Philipp: Conceptualization, Methodology, Data collection and analysis, Writing, Editing. **Aaron Zolderdo**: Methodology, Data collection and analysis, Writing, Editing. **Michael J. Lawrence**: Methodology, Data collection and analysis, Writing, Editing. **Julie E. Claussen**: Methodology, Data collection and analysis, Writing, Editing. **Liane Nowell**: Data collection and analysis, Writing, Editing. **Peter Holder**: Data collection and analysis, Writing, Editing. **Steven J. Cooke**: Conceptualization, Methodology, Data collection and analysis, Writing, Editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We would like to thank the staff at the Queen's University Biological Station for their support of the project, as well as Jordanna Bergman, Sarah Sinon, and Joseph Bernardi for assistance in the field. Funding was provided by Fisheries Conservation Foundation, US, Queens University Biological Station, Canada, and the Fish Ecology and Conservation Physiology Laboratory at Carleton University, Canada. All research was conducted in accordance with the guidelines of the Canadian Council on Animal Care as administered by Carleton University and Queen's University (B-15–08).

References

Agbeti, M.D., Kingston, J.C., Smol, J.P., Watters, C., 1997. Comparison of phytoplankton succession in two lakes of different mixing regimes. Arch. Hydrobiol. 140, 37–69.

Barthel, B.L., Cooke, S.J., Svec, J.H., Suski, C.D., Bunt, C.M., Phelan, F.J.S., Philipp, D.P., 2008. Divergent life histories among smallmouth bass *Micropterus dolomieu* inhabiting a connected river-lake system. J. Fish. Biol. 73, 829–852.

Brown, J.A., 1984. Parental care and the ontogeny of predator-avoidance in two species of centrarchid fish. Anim. Behav. 32, 113–119.

Brown, J.A., 1985. The adaptive significance of behavioural ontogeny in some. Centrarchid fishes. Environ. Biol. Fish. 13, 25–34.

Cooke, S.J., Philipp, D.P., Schreer, J.F., McKinley, S.R., 2000. Locomotory impairment of nesting male largemouth bass following catch-and-release angling. North Am. J. Fish. Manag. 20, 968–977.

Cooke, S.J., Philipp, D.P., Weatherhead, P.J., 2002. Parental care patterns and energetics of smallmouth bass (Micropterus dolomieu) and largemouth bass (Micropterus salmoides) monitored with activity transmitters. Can. J. Zool. 80, 756–777.

Cooke, S.J., Philipp, D.P., Wahl, D.H., Weatherhead, P.J., 2006. Energetics of parental care in six syntopic centrarchid fishes. Oecologia 148, 235–249.

Cooke, S.J., Twardek, W.M., Lynch, A.J., Cowx, I.G., Olden, J.D., Funge-Smith, S., et al., 2021. A global perspective on the influence of the COVID-19 pandemic on freshwater fish biodiversity. Biol. Conserv. 253, 108932.

Cushing, D.H., Kinne, O., Costlow, J.D., 1996. Towards a science of recruitment in fish populations. Oldendorf/Luhe, Ger.: Ecol. Inst. Vol. 7.

Dey, C.J., O'Connor, C.M., Gilmour, K.M., Van Der Kraak, G., Cooke, S.J., 2010. Behavioral and physiological responses of a wild teleost fish to cortisol and androgen manipulation during parental care. Horm. Behav. 58 (4), 599–605.

Diana, M.J., Larsen, A.L., Siepker, M.J., Wahl, D.H., 2012. Effects of tournament compared with catch and release angling on nest abandonment of Largemouth Bass. North Am. J. Fish. Manag. 32 (5), 832–837.

Gössling, S., Scott, D., Hall, C.M., 2020. Pandemics, tourism and global change: a rapid assessment of COVID-19. J. Sustain. Tour. 1–20.

Gravel, M.A., Cooke, S.J., 2009. Influence of inter-lake variation in natural nest predation pressure on the parental care behaviour of smallmouth bass (Micropterus dolomieu). Ethology 115 (6), 608–616.

Gross, M.L., Kapuscinski, A.R., 1997. Reproductive success of smallmouth bass estimated and evaluated from family-specific DNA fingerprints. Ecology 78, 1424–1430.

Gross, M.R., 2005. The evolution of parental care. Q. Rev. Biol. 80, 37–46.

Gwinn, D.C., Allen, M.S., 2010. Exploring population-level effects of fishery closures during spawning: an example using largemouth bass. Trans. Am. Fish. Soc. 139 (2), 626–634.

Hanson, K.C., Cooke, S.J., Suski, C.D., Philipp, D.P., 2007. Effects of different angling practices on post-release behaviour of nest guarding male black bass, *Micropterus* spp. Fish. Manag. Ecol. 14, 141–148.

Howarth, A., Jeanson, A.L., Abrams, A.E., Beaudoin, C., Mistry, I., Berberi, A., et al., 2021. COVID- 19 restrictions and recreational fisheries in Ontario, Canada: preliminary insights from an online angler survey. Fish. Res. 240, 105961.

Jackson, J.R., Einhouse, D.W., Vandevalk, A.J., Brooking, T.E., 2015. Year-Class Production of Black Bass Before and After Opening of a Spring Catch-and-Release Season in New York: Case Studies from Three Lakes, 82. American Fisheries Society Symposium,, pp. 181–191.

Keast, A., Harker, J., Turnbull, D., 1978. Nearshore fish habitat utilization and species associations in Lake Opinicon (Ontario, Canada). Environ. Biol. Fishes 3 (2), 173–184.

Kubacki, M.F., Phelan, F.J.S., Claussen, J.E., Philipp, D.P., 2002. How well does a closed season protect spawning bass in Ontario? In: Philipp, D.P., Ridgway, M.S. (Eds.), Black Bass Ecology, Conservation and Management. AFS Special Publication, Bethesda, MD US, pp. 379–386.

Lemieux, T., Milligan, K., Schirle, T., Skuterud, M., 2020. Initial impacts of the COVID-19 pandemic on the Canadian labour market. Can. Public Policy 46 (S1), S55–S65.

MacCrimmon, H.R., Robbins, W.H., 1975. Distribution of the black basses of North America. In: Stroud, R.H., Clepper, H. (Eds.), Black Bass Biology and Management. Sport Fishing Institute, Washington, DC US, pp. 56–66.

Midway, S.R., Lynch, A.J., Peoples, B.K., Dance, M., Caffey, R., 2021. COVID-19 influences on US recreational angler behavior. PLoS ONE 16 (8), e0254652. https://doi.org/10.1371/journal.pone.0254652.

Ontario OFAH 2020. https://www.ofah.org/covid19closures/ article on all of the closures during COVID.

Paradis, Y., S. Bernatchez, D. Lapointe and S.J. Cooke. In Press. Can you fish in a pandemic? An overview of recreational fishing management policies in North America during the COVID-19 crisis. Fisheries. 00:000–000.

Parkos, J.J., Wahl, D.H., Philipp, D.P., 2011. Influence of behavior and mating success on brood-specific contribution to fish recruitment in ponds. Ecol. Appl. 21, 2576–2586.

Philipp, D.P., Kaminski, C., Whitt, G.S., 1985. A comparison of the embryonic development of northern, Florida and reciprocal F1 hybrid largemouth bass in different thermal environments. Ill. Nat. Hist. Surv. Bull. 33, 261–273.

Philipp, D.P., Toline, C.A., Philipp, D.B.F., Phelan, F.J.S., 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. North Am. J. Fish. Manag. 17, 557–567.

Philipp, D.P., Claussen, J.E., Koppelman, J.B., Stein, J.A., Cooke, S.J., Suski, C.D., Wahl, D.H., Sutter, D.A.H., Arlinghaus, R., 2015. Fisheries-induced Evolution in Largemouth Bass - Linking Vulnerability to Angling, Parental Care, and Fitness, 82. American Fisheries Society Symposium,, pp. 223–234.

Pinder, A.C., Raghavan, R., Britton, J.R., Cooke, S.J., 2020. COVID-19 and biodiversity: The paradox of cleaner rivers and elevated extinction risk to iconic fish species. Aquat. Conserv.: Mar. Freshw. Ecosyst. 30 (6), 1061–1062.

Quinn, S., 2002, Status of seasonal restrictions on Black Bass fisheries in Canada and the United States. Pp 455–465 *in* Philipp, D.P., Ridgway, M.S., eds., Black Bass Ecology, Conservation and Management, AFS Special Publication No. 31, Behesda, MD US.

Quinn, S., Paukert, C., 2009. Centrarchid fisheries. In: Cooke, S.J., Philipp, D.P. (Eds.), Centrarchid Fishes – Diversity, Biology, and Conservation. John Wiley & Sons, West Sussex, UK, pp. 312–339.

Raffetto, N.S., Baylis, J.R., Serns, S.L., 1990. Complete estimates of reproductive success in a closed population of Smallmouth Bass (*Micropterus dolomieu*). Ecology 71, 1523–1535.

Ridgway, M.S., Goff, G.P., Keenleyside, M.H.A., 1989. Courtship and spawning behaviour in smallmouth bass (*Micropterus dolomieu*). Am. Midl. Nat. 122, 209–213.

Robillard, M.M., Fox, M.G., 2006. Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. Can. J. Fish. Aquat. Sci. 63, 798–809.

Rutz, C., Loretto, M.C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R.B., 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nat. Ecol. Evol. 1–4.

Scott, W.B., Crossman, E.J., 1973, Freshwater Fishes of Canada; Bulletin 184.

Shaw, S.L., Allen, M.S., 2016. Quantifying recruitment compensation in Florida largemouth bass, with implications for fisheries. Trans. Am. Fish. Soc. 145 (3), 462–475.

Siepker, M.J., Wahl, D.H., Philipp, D.P., Ostrand, K.G., 2006. Evidence of reduced reproductive success of nesting largemouth bass sampled with standard electrofishing procedures. North Am. J. Fish. Manag. 26 (3), 631–635.

Stein, J.A., Philipp, D.P., 2015. Quantifying brood predation in Largemouth Bass (*Micropterus salmoides*) associated with catch-and-release angling of nesting males. Environ. Biol. Fish. 98, 145–154.

Steinhart, G.B., Marschall, E.A., Stein, R.A., 2004. Round goby predation on Smallmouth Bass offspring in nests during simulated catch-and-release angling. Trans. Am. Fish. Soc. 133, 121–131.

Steinhart, G.B., Dunlop, E.S., Ridgway, M.S., Marshall, E.A., 2008. Should I stay or should I go? Optimal parental care decisions of a nest-guarding fish. Evolut. Ecol. Res. 10, 351–371.

Suski, C.D., Philipp, D.P., 2004. Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. Trans. Am. Fish. Soc. 133, 1100–1106.

Suski, C.D., Phelan, F.J.S., Kubacki, M.F., Philipp, D.P., 2002. The Use of Sanctuaries to Protect Nesting Black Bass from Angling, 31. American Fisheries Society Symposium,, pp. 371–378.

Suski, C.D., Svec, J.H., Ludden, J.B., Phelan, F.J.S., Philipp, D.P., 2003. The effect of catch-and-release angling on the parental care of smallmouth bass (*Micropterus dolomieu)*. Trans. Am. Fish. Soc. 132, 210–218.

Trippel, N.A., Hargrove, J.S., Leone, E.H., Austin, J.D., Allen, M.S., 2017. Angling-induced impacts on recruitment and contributions to reproduction in Florida Bass. Trans. Am. Fish. Soc. 146 (5), 871–887.

Twardek, W.M., Shultz, A.D., Claussen, J.E., Cooke, S.J., Stein, J.A., Koppelman, J.B., Phelan, F.J.S., Philipp, D.P., 2017. Potential consequences of angling on nest-site fidelity in largemouth bass. Environ. Biol. Fish. 100, 611–617.

Waters, S.D., Noble, R.L., 2004. Spawning season and nest site fidelity of largemouth bass in a tropical reservoir. North Am. J. Fish. Manag. 24, 1240–1251.

Zipkin, E., F., Sullivan, P.J., Cooch, E.G., Kraft, C.E., Shuter, B.J., Weidel, B.C., 2008. Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition. Can. J. Fish. Aquat. Sci. 66, 2279–2292.

Zolderdo, A.J., Algera, D.A., Lawrence, M.J., Gilmour, K.M., Fast, M.D., Thuswaldner, J., Cooke, S.J., 2016. Stress, nutrition and parental care in a teleost fish: exploring mechanisms with supplemental feeding and cortisol manipulation. J. Exp. Biol. 219 (8), 1237–1248.

Zolderdo, A.J., Abrams, A.E., Reid, C.H., Suski, C.D., Midwood, J.D., Cooke, S.J., 2019. Evidence of fish spillover from freshwater protected areas in lakes of eastern Ontario. Aquat. Conserv.: Mar. Freshw. Ecosyst. 29 (7), 1106–1122.

Zuckerman, Z.C., Philipp, D.P., Suski, C.D., 2014. The influence of brood loss on nest abandonment decisions in largemouth bass *Micropterus salmoides*. J. Fish. Biol. 84, 1863–1875.