

Annual recruitment is correlated with reproductive success in a smallmouth bass population

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Abstract

Annual recruitment in fish is undoubtedly impacted by a vast number of biotic and abiotic factors. That is especially the case for fish species such as the black bass (species in the genus *Micropterus*), where there is extended parental care. Although much focus has been given in the past on determining the roles that many of these factors (e.g., temperatures, wind, flow rates, and habitat change) play in determining recruitment among the black basses, little attention has been given to assessing what role reproductive success plays in that determination. To address this question, we conducted a long-term study on two adjacent smallmouth bass (SMB) *Micropterus dolomieu* Lacepède, 1802 populations in eastern ON to assess the relationship between annual fry cohort size (FCS) (i.e., population-wide reproductive success) and annual recruitment. To measure population-wide annual FCS, we used snorkel surveys to conduct a complete census of nesting SMB males during the spawn from 1990 to 2015. During those surveys, we quantified mating success, determined which nests were successful or not, and calculated the number of independent fry produced each year by summing those numbers across all successful nests. Summer snorkel surveys from 1991 to 2016 assessed annual recruitment through visual counts of age 1+ juveniles. Results demonstrated a highly significant, positive, linear relationship between annual FCS and annual recruitment.

Key words: smallmouth bass, *Micropterus dolomieu*, annual recruitment, reproductive success, angling

Introduction

Smallmouth bass (SMB) *Micropterus dolomieu* Lacepède, 1802 and largemouth bass *M. salmoides* (Lacepède, 1802), two of the species in the genus commonly referred to as black bass, are both native to much of eastern North America, including eastern ON (Macrimmon and Robbins 1975). Black bass arguably serve as the basis for the most economically important sport fishery in North America, one valued in billions of USD annually (Quinn 2002; Quinn and Paukert 2009). Developing sound, evidence-based strategies to manage and conserve these valuable natural resources serves both environmental and economic goals. During the first half of the 20th century, approaches to black bass management across a majority of jurisdictions in North America included the use of seasonal closures to angling (Paukert et al. 2007). This regulatory action was designed to protect the reproductive effort of the population during the spring spawning season,

as well as to prevent overharvest during the parental care period when male bass are extremely vulnerable to capture (Long et al. 2015). As the voluntary practice of catch and release came into increasingly common use by black bass anglers (Myers et al. 2008; Isermann et al. 2013), regulations were significantly relaxed (Paukert et al. 2007) based on the assumption that bass population dynamics would remain unaffected if all captured bass were released (Wydoski 1977). That assumption, however, has never really been tested.

Currently, the dominant paradigm concerning what controls annual recruitment in black bass populations assigns great importance to the annual variability in environmental conditions. That is, factors such as water temperature, winter duration, wind and storms, sedimentation, and water flow are viewed as major drivers of the abundance of young bass in their first year of life (see Shuter et al. 1980; Serns 1982; Parkos and Wahl 2002; Suski and Ridgway 2007; Landsman

et al. 2011). For example, favorable summer growing conditions may lead to greater cohort survival via a positive relationship between summer warmth and growth of age 0 fish (Fry and Watt 1957; Watt 1959). Similarly, longer winter durations may lead to decreased cohort survival via insufficient energy stores causing an increase in mortality of some age 0 bass (Shuter et al. 1980). It is well accepted that environmental factors can impact the survival of young bass greatly, with many of those effects likely experienced very early in life, i.e., before the parental care period is completed as well as in their first winter. The fact that SMB recruitment processes are influenced by the environment is regarded as a successful example of environmental influences on fish recruitment in general (Myers 1998). More generally, climate fluctuations as reflected in climate indices are now recognized as important in accounting for population increases or decreases of terrestrial vertebrate populations (Wan et al. 2022). Whether this is the case for SMB is unknown; however, reproductive success of individual nesting black bass, when summed across the population as a whole, may potentially play a very important role in black bass recruitment ecology. Unfortunately, that relationship has not been tested, even though that gap in our knowledge represents an important barrier to our understanding of black bass recruitment ecology, especially for SMB populations in the northern tier of its range. We propose that annual recruitment to age 1 in black bass depends upon fry cohort size (FCS), i.e., the number of surviving independent fry from all successful nests across the population. In this hypothesis, abiotic factors can still impact survival of young bass. Much of that impact, however, likely occurs during the parental care phase, thereby helping to determine FCS and subsequently age 1 abundance. This hypothesis was assessed via a long-term field study of two SMB populations in eastern ON, Canada. The long-term study incorporates winter severity using climate indices (North Atlantic Oscillation (NAO); El Niño Southern Oscillation (ENSO)) as abiotic factors that have previously been shown to affect SMB nest survival (Suski and Ridgway 2007) and more broadly population dynamics of other vertebrates (Stenseth et al. 2002; Wan et al. 2022).

Materials and methods

Study area: this study was conducted from 1990 through 2016 in a portion of the Mississippi River located in eastern ON, Canada (44°56'26.5"N, 76°41'55.0"W). The study area included two sites, the first (river site) being a 2 km section of the Mississippi River composed of a series of 8 pools connected by small rapids, terminating in 1 m falls at its outflow into Miller's Lake. The second (lake site) was Miller's Lake, a 45 ha widening of the main river with a maximum depth of about 15 m and approximately 3.5 km of shoreline. Both the river and lake sites have clearly defined littoral zones that contain bedrock, cobble, and gravel substrate interspersed with coarse woody debris and a low density of submerged aquatic vegetation. In addition, the littoral zone is moderately sloped prior to reaching a sharp drop-off to deeper water, making for a well-defined spawning area for SMB. For a full description of the study site, see Barthel et al. (2008). The

portion of the river above the two study sites is known as the Ragged Chutes, a 1 km area of very steep and turbulent flow (including barrier falls with a height of over 2 m) that prevents substantive upstream migration of SMB out of the site. The lower end of the lake site, the outflow of Miller's Lake, consists of a short series of substantial waterfalls that likely restrict both upstream and downstream migration by SMB. As a result, we have treated the populations of SMB in the two sites within the study area as separate but with some minimal mixing. We treat the overall population (both study sites combined) as a closed, self-sustaining population, with negligible natural immigration and emigration. In addition, there was no stocking of any black bass species into the study area during the 25 years of the study. Because the study area is relatively isolated from human populations, it receives very little fishing pressure, particularly during the black bass spawning season (early May through early July). During this period for each year of the study, we were regularly present conducting research and observed angling activity to be extremely low, i.e., we never encountered anglers in the river site, and less than three boats per year in the lake site, all of which were at the inflow falls fishing for species other than SMB. Besides SMB, the fish community in the study area includes rock bass *Ambloplites rupestris* (Rafinesque, 1817), pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), northern pike *Esox Lucius* Linnaeus, 1758, walleye *Sander vitreus* (Mitchill, 1818), and a number of cyprinid minnow species.

Monitoring reproductive activity: for this study, the littoral zones of the river (1990–2015) and the lake sites (1998–2015) were surveyed by teams of snorkelers every 3–5 days throughout the approximately 8-week reproductive season (early May through early July), i.e., the beginning of egg deposition until the end of parental care. During 2002, however, a series of unprecedented spring floods during the spawning season precluded safe and effective snorkeling. Because data collection was not possible during much of that season, the 2002 spawning surveys and the corresponding 2003 recruitment surveys were eliminated from the study. Aside from during the flood event, the water in both the river and the lake was very clear (Secchi disk readings of over 5 m), allowing us to see the substrate down to levels below 5 m. During the spring nesting surveys, snorkelers visually located SMB nests, marked them with a numbered tile, and recorded their locations on detailed maps of the lake and river sites. When first encountering a nest, the snorkeler recorded nest depth, a visual estimate of male total length using a 12 in. measuring standard put in the nest for accuracy (Suski and Philipp 2004), the developmental stage of the brood (used to back calculate the spawn date; Philipp et al. 1985), and mating success (a categorical score from 1 to 5 based on brood size, as described below). When a previously located nest was revisited during subsequent surveys (every 3–5 days), snorkelers documented the presence/absence of the nest-guarding parental male, identified the developmental stage of the brood, and confirmed or amended the assessment of the mating success score.

Individual male mating success (egg score): determination of male mating success (i.e., the number of fertilized eggs in the nest) followed procedures previously reported for large-

mouth bass (Stein and Philipp 2015). For that, snorkelers assigned a categorical egg score for the number of eggs deposited in the male's nest that ranged from a low of one to a high of five, based on the spread (diameter), patchiness (horizontal clustering), and saturation (vertical clustering) of the egg mass in each nest (Table 1). The egg scores from multiple visits to a single nest during the snorkeling surveys had low variability among observations, with <5% of subsequent visits showing a change in egg score. Those drops were always observed between the initial assignment of egg score and when the fry in the nest turned black and were very easily quantified. Those decreases were invariably caused by abnormally low-hatching percentages for that brood because one or both sets of gametes were less than fully viable. In those cases, we used the updated egg score to calculate the reproductive success of that nest. Once the broods reached the free-swimming stage, their numbers remained exceptionally constant throughout the rest of the parental care period. The fact that the density of brood predators in these two study areas was low certainly contributed to that stability in numbers.

Individual nesting success: to determine whether each nest was successful or not, the presence/absence of the guarding parental male and the developmental stage of the brood at each tagged nest was recorded every 3–5 days. Each nest/male was classified as successful only if the guarding male was present all the way until the brood reached the independent brown fry stage; they were considered unsuccessful if the parental male abandoned his brood or was removed from it prior to the brood reaching independence. The independent brown fry stage is characterized as when an individual fry replaces its uniform black coloration with a brown coloration and vertical darker brown bands, much like the coloration of adult SMB. Once they developed that full adult-like color pattern, they were considered independent from the parental male, i.e., they could recognize predators and avoid them (Brown 1984, 1985), a period that took 4–6 weeks post-fertilization, depending upon water temperatures.

Individual reproductive success: an individual male's reproductive success is defined as the number of offspring that survive to become independent from their parental male. That number of offspring is calculated from the observed mating success (egg score) for each brood using the conversion factors shown in Table 2. To avoid impacting the nests included in this study, those conversion factors were developed for SMB using nests outside of the study area, i.e., in Opinicon Lake, ON, using procedures previously reported for largemouth bass (Stein and Philipp 2015). Specifically, snorkelers located active SMB nests and assigned a categorical egg score (1–5) to each nest as described above. 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 black fry guarded by the male. At this point in brood development, snorkelers collected all the fry in the brood using a Fubaeli Fry Net, a triangular landing net that had been modified by replacing the standard net material with 0.5 mm mesh Nyltex 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 bot-

tle 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 Nyltex 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 FSF 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 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. The side of the net was then 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 milliliters. The total number of FSF in each brood was enumerated using a standard subsampling method whereby the number of FSF in three 10 mL aliquots of settled FSF determined the average number of FSF per settled milliliter 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 a total of 58 SMB nests sampled (9–14 nests for each egg score of 1–5). The FSF count for each egg score (and 95% confidence limit) was determined as the mean of the counts from all experimentally sampled nests as described above (Table 2).

FCS (population-wide reproductive success): annual FCS was determined for each study site (river and lake) separately by summing the reproductive success values for all individual males that completed parental care for their broods. FCS, therefore, is defined as the total number of fry that survived to independence across all of the successful nests for each study site each year. Unsuccessful nests were assigned an individual reproductive success score = 0. Excluding the flood year, 2002, FCS was calculated for the river site for each year from 1990 to 2015 and for the lake site for each year from 1998 to 2015.

Annual recruitment: we define annual recruitment as the number of offsprings that reach 1 year of age (i.e., age 1+). Relative annual recruitment for SMB was assessed for each year class produced from 1990 to 2015 by conducting a second set of snorkel surveys in the year after each respective spawning season, from late July through late August (from 1991 to 2016). For example, the relative recruitment for the 2000-year class (those fish spawned in the spring of 2000) was determined from the snorkel surveys conducted during the summer of 2001. For that, snorkelers swam the entire shoreline of either the lake or river site independently from one another, traveling at a steady rate of about 2 km/h in a line that paralleled the shoreline at a depth of 1.5–2 m that was usually about 2–4 m from shore. During those swims that lasted about 2 h, the snorkelers counted the number of age 1+ SMB

Table 1. Characteristics of the spawned egg mass that distinguish each level of the egg scoring system used in the current study.

Egg Score	Diameter (in)	Patchiness	Saturation
1	6–8	Spaces between 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

Note: Diameter is an indication of the overall spread of eggs across 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).

Table 2. Mean number of free-swimming fry (FSF) (\pm standard deviation and standard error, with 95% confidence limits) produced in experimentally sampled successful smallmouth bass *Micropterus dolomieu* nests of each egg score 1–5.

Egg Score	N	Mean fry	SD	SE	95% CI
1	12	330	111	32	70
2	13	760	215	60	130
3	11	1320	209	63	140
4	13	1940	335	93	202
5	9	2720	462	154	355

(easily identified to species and age by their orange, black, and white tricolor caudal fins and a 50–100 mm TL size class), producing an assessment of the relative annual recruitment of SMB spawned the previous year. A total of 8–12 visual assessments were conducted by 2–4 different snorkelers on at least 4 different days each year, and the relative annual recruitment for the previous year class was determined for each study site as the average number of age 1+ SMB juveniles observed during each full snorkel survey. Obviously with a study period that lasted over 25 years, the swimmers varied from year to year. Continuity in scoring/counting, however, was assured by having two of the co-authors (D. Philipp and J. Claussen) actively participate in the nesting and recruitment snorkel surveys every year.

Climate: NAO and ENSO indices are based on oceanic shifts in air pressure between Iceland and the Azores (NAO) or the extent of Pacific Equatorial warm sea surface temperatures (ENSO). They have broad influences on weather conditions (Hurrell et al. 2003) and affect both terrestrial (Wan et al. 2022) and aquatic ecosystems (Straile et al. 2003). The influence of winter NAO and ENSO can have lagged effects on populations (e.g., Halkka et al. 2006; Suski and Ridgway 2007; Zipkin et al. 2010; Wan et al. 2022).

Monthly or winter time series of NAO and ENSO climate indices were collected, respectively, from the University of East Anglia Climate Research Unit (NAO; <https://crudata.uea.ac.uk/cru/data/nao>) and National Ocean and Atmospheric Agency (ENSO; <https://www.cpc.ncep.noaa.gov/products/precip/CWlink/MJO/enso.shtml>). Positive NAO and ENSO indicate strengthening warm conditions that is important for SMB nest success (Suski and Ridgway 2007) and overwinter sur-

vival prior to age 1 (Fry and Watt 1957; Shuter et al. 1980). NAO and ENSO data were not normalized (nor adjusted based on a reference time period). Winter NAO and ENSO in year_x were used as covariates in models estimating FCS produced in year_x. Winter NAO and ENSO in year_{x+1} were used in combination with FCS from year_x to assess their relative roles in the counts of age 1+ SMB. We applied winter NAO and ENSO indices for year_{x+1} models of counts because winter severity has been shown to affect first-year survival and early cohort size of SMB (Shuter et al. 1980; Shuter and Ridgway 2002). Winter climate indices capture the winter severity known to affect the population ecology of terrestrial and aquatic organisms (Stenseth et al. 2003; Straile et al. 2003; Durant et al. 2007).

Data analysis: all data on FCS and counts of age 1+ bass were standardized (z-scores; $(x_i - x_{\text{mean}})/SD$) because detection and counts of SMB fry at nest sites and in the following summer for age 1+ bass differed in methodology and scale (i.e., 1000s for bass at nests; 10s for age 1+ bass counted by swimmers the following year). Models with standardized covariates allow for direct comparisons of coefficients as standard deviation units when explaining results. For standardized data, 0 represents the mean of variables used in analyses. All model covariates have been italicized to distinguish them from similarly labelled descriptors. For climate indices, covariate labels for winter in year_x are *NAO_yearx* and *ENSO_yearx*, and for winter in year_{x+1}, *NAO_yearx + 1* and *ENSO_yearx + 1*. The relationship evaluated in this study was the relative strength (model ranking and parameter significance) of FCS in year_x (i.e., *fry_cohort*) in predicting age 1+ SMB in year_{x+1} (i.e., *age1+_count*), with or without climate indices as covariates. Because the survey area was consistent throughout the study, total nest count (i.e., *total_nests*) and successful nest count (i.e., *success_nests*) for each year were also standardized. Nest counts (total and successful) were included in the analyses to determine the strength of these metrics in accounting for FCS and age 1+ abundance.

A general relationship between male size and nest timing in SMB (Ridgway et al. 1991; Lukas and Orth 1995) suggested that seasonal timing of nesting might potentially be important in FCS and age 1+ abundance. As a result, mean Julian date (*Julian_day*) of spawning and mean spawning season duration (*spawn_dur*; in days of the season = last nest DOY – first nest DOY) for each year were also standardized. Incorporating these covariates provides for an evaluation of the seasonal timing of nesting on patterns in FCS and abundance

of age 1+ bass. Lake or river temperature data were not continuously recorded in each year of the study, so degree-days could not be used as a covariate. Seasonal timing covariates are correlated and reflect spring warming rate ($r = -0.25$ in this study; [Ridgway and Friesen 1992](#)) and so were never included in the same model to reduce collinearity. Only one or two covariates were evaluated in any single model because of limited years in the time series and possible collinearity.

Analyses were done using general linear models ($\beta_{\text{fry_cohort OR age1+_count}} = \beta_0 + \beta_1 + \beta_2$) in the R package Bayesian regression models using Stan ([Burkner 2017](#)). Stan is a probabilistic programming language capable of modeling a wide range of functions ([Carpenter et al. 2017](#); [Stan development team 2017](#)). For each model, four chains were run, each with 2000 total iterations with the first 1000 as a burn-in period (not included), resulting in a total of 4000 posterior samples. The Rhat = 1.0 statistic was used to assess convergence (Rhat > 1.0 if chains do not converge to a common distribution; [Gelman and Rubin 1992](#)). Models were compared using the Bayesian leave one out (LOO) cross validation procedure and the leave one out information criterion (LOOIC) (“leave one out information criterion” = $-2 \times \text{ELPD}$; expected log-pointwise predictive density; [Vehtari et al. 2017](#)). Model selection follows the same conventions as model selection using ΔAIC but differs in that LOOIC ($\Delta\text{LOOIC} < 3.0$) is based on all data (and has an accompanying standard error), whereas AIC is based on data summaries. Lake and river sites were analyzed separately because of potential differences in seasonal processes such as ice formation, ice-cover duration, scouring, and spring warming that can potentially affect SMB recruitment (e.g., [Shuter et al. 1980](#)). Significance of model parameters was assessed based on whether 95% credible intervals covered 0 (i.e., not significant) or were either positive (above 0) or negative (below 0). We model-averaged those parameters found to be significant (above or below 0) in any model set using the functions “posterior_average” for β s and predictions of either fry_cohort or age1+_count in plots using “pp_average”. Model weights for averaging were based on LOOIC. We include Bayesian R^2 values for top models ([Gelman et al. 2019](#)). Bayesian R^2 is data-based and cannot be interpreted as improving fit normally associated with frequentist R^2 (variance of predicted values/variance of the data). Bayesian R^2 is an estimate of the proportion of variance explained for new data as a prior expectation of future outcomes should a study continue.

Results

Data from snorkeling surveys for quantifying reproductive activity in the spring and snorkeling surveys for quantifying relative recruitment in late summer the following year are summarized for the river site ([Table 3](#)) and the lake site ([Table 4](#)) of the study area. Over the 25-year duration of this study, excluding 2002 in which a flood prevented data collection, we monitored a total of 3109 SMB nests, 2082 in the river site from 1990 to 2015, and 1027 in the lake site from 1998 to 2015.

Timing of the egg-laying period: although the average date of first eggs laid was 19 May in the lake site and 20 May in the river site ([Tables 3 and 4](#)), it ranged from as early as 11 May (in 1998) to as late as 1 June (in 1997). In fact, the 1998 egg-laying period (first eggs laid to last eggs laid in a year), which lasted 11–25 May, ended six days earlier than when the first eggs were laid the previous year (1 June). The duration of the egg-laying period was as short as 13 days (in 2011) and as long as 25 days (in 2000). Although there was temporal variation in the onset and duration of the egg-laying periods across the years of the study ([Figs. 1A and 2A](#)), in any given year the egg-laying periods at the two sites were similar in their timing; that is, comparing the two sites (river vs. lake), the onset and duration of egg laying differed by no more than 1 day in any given year ([Tables 3 and 4](#)).

Nesting activity/success: the total number of nests constructed that received at least some eggs also varied greatly across years in both sites ([Figs. 1B and 2B](#)). For each of the years in which we monitored both the lake site and the river site (1998–2015), there were more total nests in the river site than in the lake site, with an overall annual average of 83 nests (SD = 29.6, range = 37–142) in the river site compared to an average of 60 nests (SD = 16.8, range 30–97) in the lake site. The number of successful nests (i.e., those nests where males successfully raised broods to independence) was also higher in the river site compared to the lake site, with an overall average of 62 successful nests (SD = 22.5, range = 30–114) in the river site compared to 50 successful nests (SD = 14.2, range 27–87) in the lake site ([Figs. 1C and 2C](#)). Finally, the annual nesting success (% of total nests that were successful at raising broods) varied substantially across the years as well, from a high of 94% to a low of 44% in the river site and a high of 94% to a low of 65% in the lake site ([Figs. 1D and 2D](#)).

FCS: FCS fluctuated widely across years. Levels of successful fry production varied among years almost six-fold in the river site ([Fig. 1E](#)), from a low of 20 200 in 2010 to a high of 115 300 in 2006 and almost four-fold in the lake site ([Fig. 2E](#)), from a low of 34 400 in 2011 to a high of 111 000 in 2001.

Annual recruitment: relative annual recruitment, determined by visual counts of 1-year old individuals observed during summer snorkel surveys, varied substantially across years for both sites ([Tables 3 and 4](#)), ranging from 21 to 111 in the river site and from 30 to 124 in the lake site.

Relationship between Nesting success and FCS: Bayesian regression model for the lake and river sites were partitioned into those predicting FCS or predicting age 1+ counts. For both lake and river sites, the number of successful nests (i.e., those with broods reaching independence) as a single covariate, or combined with a seasonal timing parameter (spawn_dur for the lake site; Julian_day for the river site), were top models and were within the top-ranked models for both lake and river model sets ([Table 5](#)). For the lake site, climate indices alone or with success_nests were ranked low, while for the river site, ENSO_DJF was included in the second rank model ([Table 5](#)).

The parameter estimates in the top models incorporating success_nests from [Table 5](#) show a significant success_nests effect for both the lake and river sites ([Table 6](#)). Slopes describing the relationship between success_nests and fry_cohort

Table 3. Results of the 1990–2015 smallmouth bass *Micropterus dolomieu* snorkel surveys in the river site (Mississippi River).

Year	Number of total nests	Number of nests (%) successful	FCS (number of fry)	#1+ SMB observed	Date of 1st spawn	Days of egg laying
1990	37	33 (89%)	35 300	22	28 May	18
1991	63	55 (87%)	42 600	24	15 May	13
1992	70	57 (81%)	51 100	56	23 May	20
1993	43	30 (70%)	28 900	28	31 May	15
1994	73	56 (77%)	80 200	93	31 May	16
1995	105	88 (84%)	95 500	39	23 May	16
1996	75	66 (88%)	79 300	39	25 May	23
1997	72	60 (83%)	89 800	111	1 June	14
1998	74	64 (86%)	62 400	69	11 May	14
1999	63	59 (94%)	60 300	34	13 May	18
2000	82	36 (44%)	25 200	21	20 May	25
2001	94	65 (69%)	70 700	71	17 May	20
2003	69	64 (93%)	82 300	83	18 May	22
2004	78	72 (92%)	72 300	52	16 May	22
2005	130	114 (88%)	101 600	78	21 May	16
2006	141	110 (78%)	115 300	107	14 May	20
2007	104	90 (86%)	48 900	36	17 May	15
2008	142	68 (48%)	71 300	36	19 May	24
2009	131	61 (47%)	58 800	46	17 May	21
2010	58	37 (64%)	20 200	24	13 May	20
2011	40	30 (75%)	52 400	61	26 May	13
2012	82	49 (60%)	65 400	53	19 May	20
2013	63	38 (60%)	26 300	33	21 May	21
2014	87	78 (90%)	71 800	65	28 May	16
2015	106	77 (73%)	80 400	79	24 May	16
Total	2082	1557	1 588 300	NA		
Average	83.3	62.3	63 532	54.3	20 May	18.3
SD	29.6	22.5	26 111	26.5		

Note: Data shown include direct counts by snorkelers of the total number of smallmouth bass nests, as well as the number and percentage of those nests that were successful in producing independent broods. The annual fry cohort size (FCS) for the river site (the number of independent fry produced from all successful nests) was calculated as described in methods using means of fry counts sampled for each egg score to determine the number of fry from each successful nest and then summing those fry numbers across all successful nests for that year. Relative recruitment (the number of 1+ smallmouth bass observed during the summer snorkel surveys of the entire shoreline of the site) was determined directly from the summer snorkel survey counts. The onset and duration of egg laying (i.e., the actual spawning component of the reproductive season) are provided as well.

were positive and overlapping for lake and river sites but steeper for the river site. Credible intervals for the success_nests slope parameter at the river site included 1.0 but not for the lake site (Table 6). The parameter ENSO_DJF in the second-ranked model was not significant. Considering the high ranks for models with success_nests and a seasonal timing parameter and low-rank or non-significant parameter estimates for models with climate indices, we conclude the contribution of climate indices in the preceding winter had little effect on within-year fry cohort production at the population level.

As a result, a unit increase in the number of successful nests in both sites results in a near unit increase in FCS with the river site providing a stronger match between the two variables based on a steeper slope and credible intervals covering 1.0. From the top models, the seasonal timing covariate for the lake site (spawn_dur) was not significant (CI covering 0; Table 6), but the seasonal timing covariate for the river site (Julian_day) was positive and significant (CI not covering 0; Table 6). The positive coefficients point to later seasonal nest-

ing with a shorter duration of spawning days as assisting total fry production.

Because success_nests was in almost all top models ($\Delta\text{LOOIC} < 3.0$), we model averaged success_nests across all ranked models in Table 5 to generate a general estimate of the relationship between success_nests and fry_cohort. For both sites, this relationship was positive and significant, indicating that increasing numbers of successful nests result in increased FCS. For the lake site, the model-averaged coefficient (β ; 95% credible intervals) for success_nests ($\beta = 0.575$; 0.246, 0.913) was lower than that for the river site ($\beta = 0.789$; 0.554, 1.023). The relationships predicting FCS based on the model-averaged number of successful nests (i.e., success_nests) for lake and river sites are summarized in Figure 3. Because data were standardized, 0 represents the mean of each variable. The relatively greater strength of this relationship for the river site, when compared to the lake site, can be seen by the narrower credible intervals and greater slope.

Relationship between FCS and recruitment: model performance of lake and river sites showed that FCS, as a predictor

Table 4. Results of the 1998–2015 smallmouth bass *Micropterus dolomieu* snorkel surveys in the lake site (Millers Lake).

YEAR	Number of total nests	Number of nests (%) successful	FCS (number of fry)	Number of 1+ SMB observed	Date of 1st spawn	Days of egg laying
1998	47	43 (91%)	54 000	60	11 May	14
1999	60	54 (90%)	62 600	72	13 May	18
2000	71	57 (80%)	65 300	31	20 May	25
2001	97	87 (89%)	111 000	124	17 May	20
2003	63	59 (94%)	87 900	57	18 May	22
2004	42	39 (93%)	52 900	70	17 May	21
2005	70	58 (83%)	76 500	84	21 May	16
2006	64	45 (70%)	55 700	74	14 May	20
2007	50	40 (80%)	48 200	65	17 May	15
2008	52	48 (92%)	53 200	47	19 May	24
2009	84	52 (62%)	51 100	81	17 May	21
2010	41	30 (73%)	45 700	52	14 May	19
2011	63	41 (65%)	34 400	30	26 May	13
2012	30	27 (90%)	43 800	43	19 May	20
2013	53	44 (83%)	39 000	39	21 May	21
2014	62	53 (85%)	60 500	72	28 May	16
2015	78	67 (86%)	73 500	70	21 May	14
Total	1027	844	1 015 300	NA		
Average	60.4	50 (83%)	59 724	63	19 May	18.8
SD	16.8	14.2	19 040	22.9		

Note: Data shown include direct counts by snorkelers of the total number of smallmouth bass nests, as well as the number and percentage of those nests that were successful in producing independent broods. The annual fry cohort size (FCS) for the lake site (the number of independent fry produced from all successful nests) was calculated as described in methods using means of fry counts sampled for each egg score to determine the number of fry from each successful nest and then summing those fry numbers across all successful nests for that year. Relative recruitment (the number of 1+ smallmouth bass observed during the summer snorkel surveys of the entire shoreline of the site) was determined directly from the summer snorkel survey counts. The onset and duration of egg laying (i.e., the actual spawning component of the reproductive season) are provided as well.

of age 1+ counts in the year following nesting, was included in all top-ranked models and for several models below the top-ranked model (Table 7). FCS alone is the top-ranked model for the lake site with seasonal spawning covariates included in second- and third-ranked models. For the river site, FCS and models with seasonal spawning covariates were ranked lower than models where climate indices were included and resulted in the top-ranked models. Climate indices clearly have a different influence between lake and river sites in contributing to age 1+ counts.

For the lake site, climate indices were low-ranked with no support when alone or in combination with fry_cohort. Coefficients (β s) for climate indices were not significant in the lake model set (Table 8). In contrast, coefficients for climate indices were significant and positive for the top-ranked models in the river model set (Table 8). For the river site, this result points to the influence of climate indices in the winter after fry cohorts are produced and before age 1+ counts are made in the field the following summer.

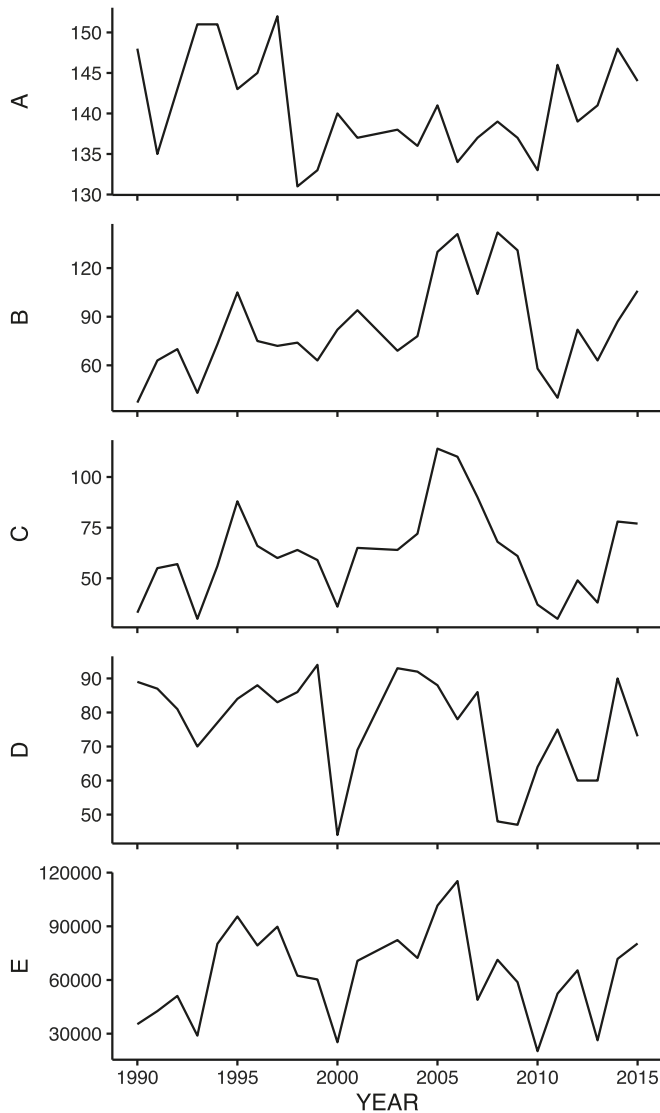
For lake and river sites, slopes describing the relationship between the FCS and age 1+ bass were positive, similar (lake and river sites: $\beta_1 > 0.70$), and significant, with 95% credible intervals, including 1.0 in all but one model (Table 8). Bayesian R^2 estimates for the lake and river sites point to an expectation of good model performance for new data relating fry_cohort to age1+_count (Table 8; Bayesian $R^2 \approx 0.5$ – 0.65).

Because fry_cohort was significant and in the top models predicting age1+_count ($\Delta\text{LOOIC} < 3.0$), we model-averaged

fry_cohort across all ranked models in Table 7 to generate a general estimate of the relationship between fry_cohort and age1+_count. For both sites, this relationship was positive and significant, indicating that an increase in FCS results in increased counts of age 1+ bass. For the lake site, the model-averaged coefficient (β ; 95% credible intervals) for fry_cohort ($\beta = 0.700$; 0.278, 1.113) overlapped with that of the river site ($\beta = 0.788$; 0.485, 1.091). The relationship predicting age 1+ counts based on the model-averaged FCS (i.e., fry_cohort) for lake and river sites are summarized in Fig. 4. Again, as in Fig. 3, the river site has narrower credible intervals than the lake site.

Examining a sample of successive years in Fig. 4, which includes years with the largest residuals, reveals important differences between the two sites. First, large residuals at each site did not occur in the same year. Secondly, the relative position of successive years and their residuals differed between the two sites. The relationship between FCS and age 1+ count index at the lake site swung widely in the 2001–2003 period (2002 is excluded; see Methods), whereas this pattern occurred in the river site during the 1995–1998 period (see Fig. 4). Site-specific differences in the effects of climate indices (Tables 7 and 8) between river and lake sites suggest that abiotic processes influencing river cohorts of young SMB differ from those processes in lakes, perhaps both in kind and scale of effect since climate indices were relatively unimportant in the lake site.

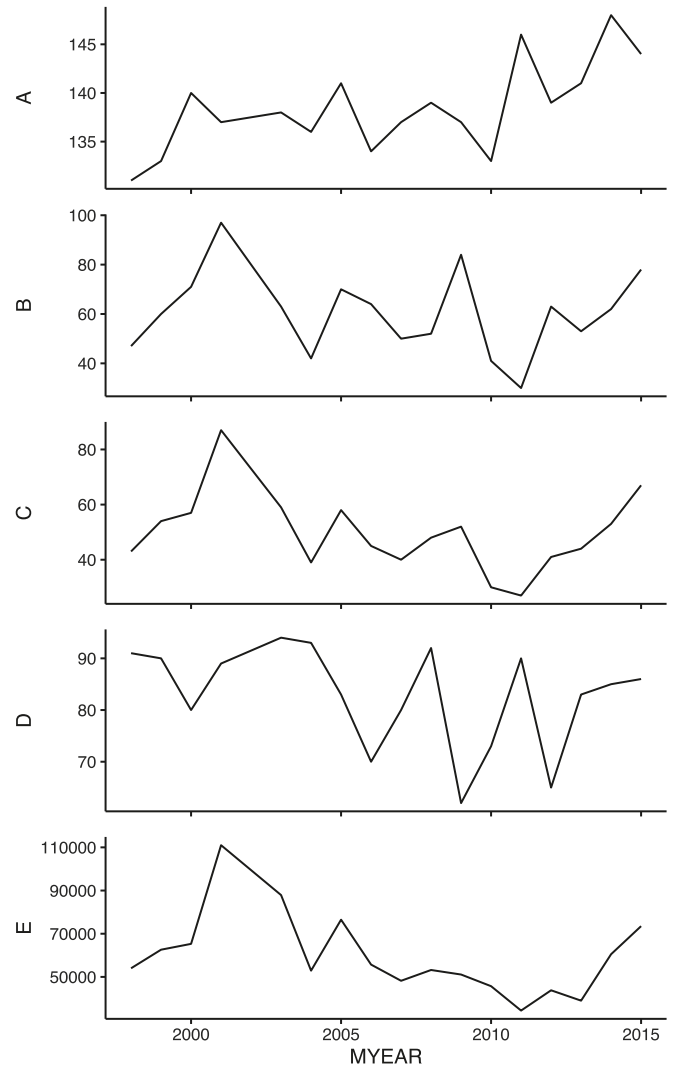
Fig. 1. Annual smallmouth bass *Micropterus dolomieu* spawning characteristics (1990–2015) for the river site. Each panel shows the relative values across the study years for the following metrics: (A) date of onset of spawning (Julian date of first eggs laid), (B) total number of nests that received eggs, (C) number of nests that successfully produced broods that developed to independence, (D) percentage of nests that produced successful broods, and (E) relative annual recruitment in number of 1+ smallmouth bass counted in snorkel surveys of total shoreline.



Discussion

It is widely accepted that a long list of environmental factors can influence annual recruitment in fish species (see [Beverton and Holt 1957](#); [Walters and Martell 2004](#)). It is also clear that recruitment is a very complex process, particularly for fish species that have obligatory parental care like the SMB for which extended paternal protection from brood predators is necessary for early offspring survival ([Brown 1984, 1985](#); [Ridgway et al. 1989](#); [Gross 2005](#); [Cooke et al. 2006](#); [Barthel et al. 2008](#)). From the outset, however, our premise has been that for SMB many of these environmental drivers

Fig. 2. Annual smallmouth bass *Micropterus dolomieu* spawning characteristics (1998–2015) for the lake site. Each panel shows the relative values across the study years for the following metrics: (A) date of onset of spawning (Julian date of first eggs laid), (B) total number of nests that received eggs, (C) number of nests that successfully produced broods that developed to independence, (D) percentage of nests that produced successful broods, and (E) relative annual recruitment in number of 1+ smallmouth bass counted in snorkel surveys of total shoreline.



could be influencing spawning and early parental care activities, thereby affecting recruitment very early in the life cycle by impacting reproductive success. If that is the case, then reproductive success across the population may be an accurate predictor of recruitment and as a result is more of a focal target for management. Specifically, our hypothesis proposes that the annual recruitment of age 1+ SMB depends on the annual FCS, i.e., the total number of fry produced in the population that survived beyond the parental care period to become independent of their guardian parental male. Environmental influences on age 1+ recruitment as represented by climate indices have been shown to be in-

Table 5. Model selection results for models predicting smallmouth bass *Micropterus dolomieu* fry cohort size of the form $\beta_{\text{fry_cohort}} = \beta_0 + \beta_1 + \beta_2$.

Model covariates	LOOIC	Δ LOOIC
Lake		
success_nests + spawn_dur	43.79	0
success_nests	44.80	1.01
total_nests	45.01	1.22
success_nests + ENSO_yearx	46.27	2.48
success_nests + Julian_day	46.34	2.55
success_nests + NAO_yearx	46.89	3.10
ENSO_yearx	54.54	10.75
NAO_yearx	54.83	11.04
River		
success_nests + Julian_day	45.36	0
success_nests + ENSO_yearx	48.11	3.45
success_nests	49.20	3.84
success_nests + spawn_dur	51.09	5.73
success_nests + NAO_yearx	51.73	6.37
total_nests	62.34	16.98
ENSO_yearx	73.83	28.47
NAO_yearx	74.62	29.26

Note: Lake and river sites were analyzed separately. Covariates were standardized except for NAO and ENSO indices. NAO_yearx and ENSO_yearx represent winter NAO and ENSO indices, respectively.

fluent at this latitude (Suski and Ridgway 2007) but how influential relative to FCS has now been assessed in this study.

The current 25-year study on the reproductive history of two SMB study populations in eastern ON was designed to test our hypothesis, and the results of the study clearly support it; annual recruitment, defined as the number of 1+ individuals, (age1+_count) in both SMB populations were tightly correlated with annual FCS (i.e., the number of independent fry produced; fry_cohort). Using general indices of adult abundance fails to serve as a surrogate for FCS because the number of actual breeding adults is often only a small and variable proportion of the overall number of adults in the population (Raffeto et al. 1990; Ridgway et al. 1991; Franckowiak et al. 2017). Furthermore, even the total number of nests does not occur in any of the top-ranked models accounting for FCS (Table 5), meaning that using either total adult abundance or total numbers of nests built (or both) as a surrogate for reproductive success does not have sufficient power to detect an influence on recruitment. In addition, it takes substantial effort to gather data from enough years to build a robust time series database capable of assessing these types of relationships, and conclusions based on short time series can often be misleading (Weatherhead 1986; May 1999). Unfortunately, long-term ecological research studies are uncommon (Franklin 1989) despite their ability to reveal ecological mechanisms and patterns that would otherwise go unnoticed (Magnuson 1990; Lindenmayer et al. 2012). The study reported herein involved collecting data that required 25 years of snorkeling.

The inclusion of climate indices (winter NAO; winter ENSO), previously shown to be important parameters in nest survival for SMB (Suski and Ridgway 2007) and more widely in other vertebrate populations (Wan et al. 2022), influenced ranking models predicting counts of age 1+ bass but only when they were combined with fry_cohort. Because both climate indices alone ranked low with little to no weight in model selection, they are not important at predicting recruitment as single covariates. Suski and Ridgway (2007) (their fig. 2) showed the influence of positive values of winter NAO and ENSO on thermocline depth (deepening) and lake temperature gradient (shallowing) through the epilimnion and metalimnion during the following summer. In turn, these temperature effects influenced individual nest survival and presumably FCS of the population. In the current study, climate indices for the winter after the formation of a fry cohort (the first winter for the juvenile SMB) were important only for the river site by contributing to fry cohort size as a predictor of age 1+ counts (Tables 7 and 8). Climate Indices did not contribute to better predictions at the lake site (Tables 5 and 6). This outcome likely reflects a difference between river and lake populations of SMB in the kind and severity of abiotic factors that they experience in their first year of life. Positive coefficients for the climate indices at the river site (Table 8) suggest that abiotic factors such as wind and its implications for winter severity, ice stability, spring flows, wind chill, or snow cover may influence age 1+ counts in rivers more substantially than in lakes (Suski and Ridgway 2007).

As a corollary to our main hypothesis, we propose that reductions in the reproductive success of individual male SMB, including nest destruction from storms (Goff 1986) or human activities (Wagner et al. 2006), arrested development of the embryos from cold temperatures, (Philipp et al. 1985), overwinter severity (Shuter et al. 1980), as well as angling-induced disruptions to the male's parental care (Philipp et al. 1997; Cooke et al. 2000; Suski et al. 2003; Hanson et al. 2007; Steinhart et al. 2008; Zuckerman and Suski 2013; Zuckerman et al. 2014; Stein and Philipp 2015), would result in a reduction in that population's FCS. That reduction would then cause a concomitant reduction in the recruitment of 1+ individuals the following year. Such a result would have clear implications for angling and its management.

The results of an extraordinarily serendipitous experiment made possible by the recent (and hopefully singular) COVID pandemic confirmed that such a result is indeed the case (Philipp et al. 2022). That study compared for both SMB and largemouth bass the annual FCS (i.e., the number of independent fry produced at the population level) with recruitment of age 1+ juveniles in years before (2019), during (2020–21), and after (2022) the pandemic in Opinicon Lake, ON. During the pandemic, in May–June of 2020 and 2021, foreign tourists were prohibited from entering Canada, local cottagers were discouraged from visiting their vacation homes to reduce strain on rural health care facilities, and most boat ramps and marinas were closed. As a result, angling during the bass spawning season was almost non-existent in many lakes within the area. Conversely, the angling pressure on nesting male bass was extremely high in 2019 before the pan-

Table 6. Model parameters (95% credible intervals, CI) for the top models predicting smallmouth bass *Micropterus dolomieu* fry cohort size at nest sites (fry_cohort) for lake and river sites (model selection in Table 5).

Models	β_0	β_1	β_2	Bayesian R^2
Lake				
Int + success_nests + spawn_dur	-0.191 (-0.584, 0.215)	0.592 (0.265, 0.914)	0.245 (-0.159, 0.654)	0.505 (0.176, 0.667)
Int + success_nests	-0.178 (-0.601, 0.258)	0.558 (0.219, 0.883)		0.446 (0.095, 0.629)
River				
Int + success_nests + Julian_day	-0.0001 (-0.231, 0.231)	0.791 (0.558, 1.020)	0.262 (0.026, 0.490)	0.692 (0.509, 0.773)
Int + success_nests + ENSO_DJF	-0.0116 (-0.253, 0.226)	0.795 (0.549, 1.037)	-0.148 (-0.393, 0.101)	0.649 (0.454, 0.741)
Int + success_nests	-0.0013 (-0.241, 0.245)	0.766 (0.512, 1.021)		0.623 (0.402, 0.728)

Note: Bayesian R^2 is an estimate of the proportion of variance explained for new data (95% credible interval). Model covariates and corresponding parameter estimates are provided in sequence using the form $\beta_{\text{fry_cohort}} = \beta_0 + \beta_1 + \beta_2$.

Fig. 3. The model-averaged relationship between the number of successful nests (success_nests) and cohort size of young smallmouth bass *Micropterus dolomieu* (fry_cohort). Model averaging was across all models with success_nests (β , 95% credible intervals) as a covariate. Cohort size was determined at late-stage parental care: 1998–2015 for the lake site (top panel; $\beta = 0.575$ (0.246, 0.913)) and 1990–2015 for the river site (bottom panel; $\beta = 0.789$ (0.554, 1.023)).

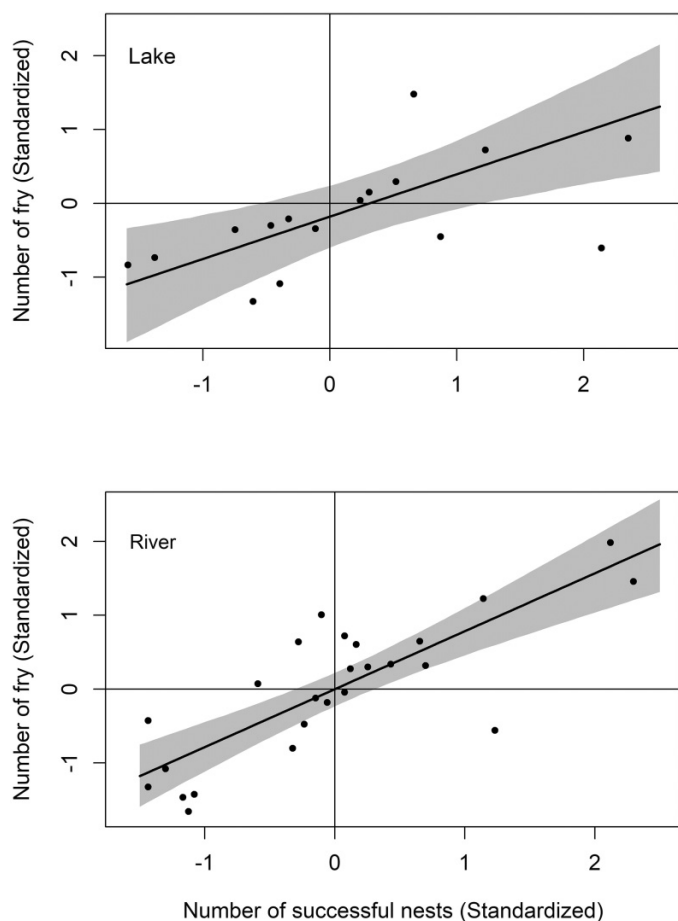


Table 7. Model selection results for models predicting the number of age 1+ smallmouth bass *Micropterus dolomieu* of the form $\beta_{\text{age1+count}} = \beta_0 + \beta_1 + \beta_2$.

Model covariates	LOOIC	Δ LOOIC
Lake		
fry_cohort	42.60	0
fry_cohort + spawn_dur	43.68	1.08
fry_cohort + Julian_day	43.99	1.39
fry_cohort + ENSO_yearx + 1	44.55	1.95
success_nests + Julian_day	44.75	2.15
success_nests	44.93	2.33
fry_cohort + NAO_yearx + 1	45.92	3.32
total_nests + Julian_day	46.06	3.46
total_nests	47.26	4.66
success_nests + spawn_dur	48.33	5.73
total_nests + spawn_dur	50.91	8.31
ENSO_yearx + 1	51.38	8.78
NAO_yearx + 1	54.23	11.63
River		
fry_cohort + NAO_yearx + 11	50.96	0
fry_cohort + ENSO_yearx + 1	52.36	1.40
fry_cohort	55.13	4.17
fry_cohort + Julian_day	55.48	4.52
fry_cohort + spawn_dur	55.86	4.90
success_nests + Julian_day	66.73	15.77
success_nests	69.83	18.87
ENSO_yearx + 1		19.79
success_nests + spawn_dur	70.90	19.94
total_nests + Julian_day	72.14	21.18
total_nests	73.11	22.15
total_nests + spawn_dur	73.11	22.15
NAO_yearx + 1	74.17	23.21

Note: Lake and river sites were analyzed separately. All covariates were standardized except for NAO and ENSO indices. NAO_yearx + 1 and ENSO_yearx + 1 represent winter NAO and ENSO indices in the winter prior to age 1 counts, respectively.

demographic and also in 2022 when tourists returned. As our hypothesis predicted, the annual FCS and annual recruitment of age 1+ fish for the year classes during two non-pandemic

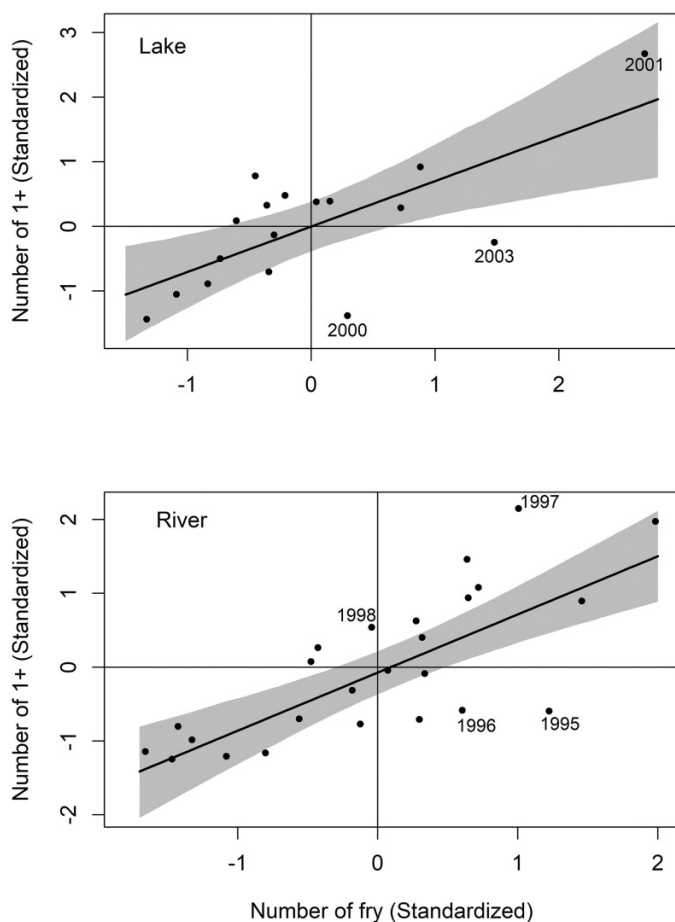
years (2019 and 2022) was almost zero, whereas those values for the two pandemic years when angling pressure was low (2020–21) were the highest ever recorded since records began in 1990.

Table 8. Model parameters (95% credible intervals) for the top models predicting age 1+ smallmouth bass *Micropterus dolomieu* abundance in year $x + 1$ (age1+_count) for lake and river sites (model selection in Table 7).

Models	β_0	β_1	β_2	Bayesian R^2
Lake				
Int + fry_cohort	0.0017 (−0.387, 0.402)	0.704 (0.314, 1.10)		0.468 (0.131, 0.650)
Int + fry_cohort + spawn_dur	0.0004 (−0.379, 0.388)	0.733 (0.330, 1.114)	−0.214 (−0.618, 0.199)	0.515 (0.193, 0.672)
Int + fry_cohort + Julian_day	0.0065 (−0.377, 0.392)	0.708 (0.295, 1.117)	−0.178 (−0.586, 0.248)	0.504 (0.180, 0.668)
River				
Int + fry_cohort + NAO_yearx + 1	−0.130 (−0.401, 0.149)	0.827 (0.553, 1.104)	0.226 (0.037, 0.417)	0.648 (0.444, 0.744)
Int + fry_cohort + ENSO_yearx + 1	−0.009 (−0.261, 0.237)	0.718 (0.420, 0.998)	0.237 (0.006, 0.468)	0.623 (0.420, 0.725)
Int + fry_cohort	−0.003 (−0.279, 0.287)	0.774 (0.486, 1.105)		0.553 (0.297, 0.685)
Int + fry_cohort + Julian_day	−0.0006 (−0.280, 0.280)	0.758 (0.479, 1.055)	0.190 (−0.091, 0.501)	0.588

Note: Bayesian R^2 is an estimate of the proportion of variance explained for new data (95% credible interval). Model covariates and corresponding parameter estimates are provided in sequence using the form $\beta_{\text{age1+_count}} = \beta_0 + \beta_1 + \beta_2$.

Fig. 4. The model-averaged relationship between cohort size of young smallmouth bass *Micropterus dolomieu* under late-stage parental care (fry_cohort) and total abundance of age 1+ smallmouth bass the following year (age1+_count). Model averaging was across all models with fry_cohort (β , 95% credible intervals) as a covariate. Abundance of age 1+ bass was based on summer index survey swims: 1998–2015 for the lake site (top panel; $\beta = 0.70$ (0.278, 1.113)) and 1990–2015 for the river site (bottom panel; $\beta = 0.788$ (0.485, 1.091)).



We argue that the results from our current study combined with past studies support the supposition that angling for nesting bass can have a negative impact on the size of the cohort of independent fry produced that year, and that would then translate into a reduction in population-wide annual recruitment. We and others (Philipp et al. 1997; Cooke et al. 2000; Suski et al. 2003; Hanson et al. 2007; Steinhart et al. 2008; Zuckerman et al. 2014) have previously demonstrated that angling an individual nesting male bass reduces its reproductive success to zero if that male is harvested or even released in a way that causes the male to abandon its nest (e.g., released some distance from his nest or after some time has elapsed). That reduction in reproductive success is the result of partial-to-total predation of the brood (Zuckerman and Suski 2013; Stein and Philipp 2015). Males that have suffered a substantial enough loss of brood make the evolutionary decision (Williams 1966) to abandon the remaining brood when its fitness value has decreased to the point where it is better to wait until future breeding opportunities rather than invest in the current brood (Zuckerman et al. 2014). Even if the male does return and resumes parental care, there is often some loss of offspring to predation by surrounding predators during his absence (Philipp et al. 1997; Gravel and Cooke 2009; Stein and Philipp 2015) or from the lack of aeration of egg-sac fry during the temporary absence of the parental male (Scott and Crossman 1973; Neves 1975).

Admittedly, our studies have for the most part been restricted to populations located close to their northern extreme. As a result, how applicable these results are to populations farther south where seasonal climate conditions are quite different is currently unknown and certainly begs more research. Studies of Florida bass *M. floridanus* (Lasueur, 1822) populations (Rogers and Allen 2009; Allen et al. 2011; Shaw and Allen 2014, 2016; Trippel et al. 2017) have measured many of the same spawning and recruitment metrics that we used in this study. This species shares many parental care behaviors and life history traits with its close relative, the largemouth bass, as well as with its more distantly related relative, the SMB, but has a climatically very different native range (peninsular FL). Florida bass have adapted some of their spawning characteristics to the longer growing seasons encountered in FL, i.e., a greatly extended duration

of the egg-laying period (first eggs spawned until last eggs spawned), lasting from January through May (a period as long as 150 days or more) across much of its range. The SMB egg-laying period in our study populations was as short as 13 days and no longer than 25 days. Compared to the more northerly populations of SMB in our study, an extended spawning season provides the Florida bass with a much greater window for re-nesting and re-spawning following an unsuccessful first (or even second or third) attempt. Although studies in FL reported levels of nesting success and reproductive success among individual males similar to what we observed; the relationship between reproductive success and recruitment was not so clear. The fact that Florida bass also produced multiple broods through the season with reduced brood sizes relative to the more northerly largemouth bass (Sutter et al. 2014) may indicate they employ a somewhat different life history strategy.

That said, our results are unlikely to be simply strange or unique to a fringe population located in some atypical habitat. It is more likely that any population of black bass could suffer substantive reductions in annual recruitment of 1+ age individuals when the level of disturbance to its reproductive effort via any natural or human-induced reason (including angling) is high enough to markedly reduce individual reproductive success across many individuals and, therefore, the FCS of that population. We would urge natural resource agencies to investigate that possibility in their areas. Furthermore, for populations where recruitment is found to be reduced or non-existent and some form of management intervention is desired, the protection of spawning bass offers a long-neglected alternative to stocking hatchery fingerlings to “correct a missing year class”. This type of creative and evidence-informed approach has the potential to revolutionize the management of recreational fisheries (Brownscombe et al. 2019) and may be overdue within the bass management community.

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References

- Allen, M.S., Rogers, M.W., Catalano, M.J., Gwinn, D.G., and Walsh, S.J. 2011. Evaluating the potential for stock size to limit recruitment in largemouth bass. *Trans. Am. Fish. Soc.* **140**: 1093–1100. doi:[10.1080/00028487.2011.599259](https://doi.org/10.1080/00028487.2011.599259).
- Barthel, B.L., Cooke, S.J., Svec, J.H., Suski, C.D., Bunt, C.M., Phelan, F.J.S., and Philipp, D.P. 2008. Divergent life histories among smallmouth bass, *Micropterus dolomieu*, inhabiting a connected river–lake system. *J. Fish Biol.* **73**: 829–852. doi:[10.1111/j.1095-8649.2008.01972.x](https://doi.org/10.1111/j.1095-8649.2008.01972.x).
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. *Fishery Investigation Series*. U.K. Ministry of Agriculture and Fisheries.
- Brown, J.A. 1984. Parental care and the ontogeny of predator-avoidance in two species of Centrarchid fish. *Anim. Behav.* **32**: 113–119. doi:[10.1016/S0003-3472\(84\)80329-2](https://doi.org/10.1016/S0003-3472(84)80329-2).
- Brown, J.A., 1985. The adaptive significance of behavioural ontogeny in some Centrarchid fishes. *Environ. Biol. Fishes.* **13**: 25–34. doi:[10.1007/BF00004853](https://doi.org/10.1007/BF00004853).
- Brownscombe, J.W., Hyder, K., Potts, W., Wilson, K.L., Pope, K.L., Danylchuk, A.J., et al. 2019. The future of recreational fisheries: advances in science, monitoring, management, and practice. *Fish. Res.* **211**: 247–255. doi:[10.1016/j.fishres.2018.10.019](https://doi.org/10.1016/j.fishres.2018.10.019).

- Bürkner, P.C. 2017. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**: 1–28. doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01).
- Carpenter, B., Gelman, A., Hoffman, M., Lee, D., Goodrich, B., Betancourt, M., and Riddell, A. 2017. Stan: a probabilistic programming language. *J. Stat. Softw.* **76**: 1–32. doi:[10.18637/jss.v076.i01](https://doi.org/10.18637/jss.v076.i01). PMID: [36568334](https://pubmed.ncbi.nlm.nih.gov/36568334/).
- Cooke, S.J., Philipp, D.P., Schreer, J.F., and McKinley, R.S. 2000. Locomotor impairment of nesting male largemouth bass following catch-and-release angling. *North Am. J. Fish. Manage.* **20**: 968–977. doi:[10.1577/1548-8675\(2000\)020%3c0968:LIONML%3e2.0.CO;2](https://doi.org/10.1577/1548-8675(2000)020%3c0968:LIONML%3e2.0.CO;2).
- Cooke, S.J., Philipp, D.P., Wahl, D.H., and Weatherhead, P.J. 2006. Energetics of parental care in six syntopic centrarchid fishes. *Oecologia*, **148**: 235–249. doi:[10.1007/s00442-006-0375-6](https://doi.org/10.1007/s00442-006-0375-6). PMID: [16485098](https://pubmed.ncbi.nlm.nih.gov/16485098/).
- Durant, J.M., Hjermann, D.O., Ottersen, G., and Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**: 271–283.
- Franckowiak, R., Ridgway, M., and Wilson, C. 2017. Genetic mating system and mate selection in smallmouth bass. *Ecol. Evol.* **7**(21): 8864–8875. doi:[10.1002/ece3.3423](https://doi.org/10.1002/ece3.3423). PMID: [29152183](https://pubmed.ncbi.nlm.nih.gov/29152183/).
- Franklin, J.F. 1989. Importance and justification of long-term studies in ecology. In *Long-term studies in ecology*. Edited by G.E. Likens. Springer, New York, NY. pp. 3–19.
- Fry, F.E.J., and Watt, K.E.F. 1957. Yields of year classes of the smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. *Trans. Am. Fish. Soc.* **85**: 135–143. doi:[10.1577/1548-8659\(1955\)85%5b135:YOYCOT%5d2.0.CO;2](https://doi.org/10.1577/1548-8659(1955)85%5b135:YOYCOT%5d2.0.CO;2).
- Gelman, A., and Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**: 457–472. doi:[10.1214/ss/1177011136](https://doi.org/10.1214/ss/1177011136).
- Gelman, A., Goodrich, B., Gabry, J., and Vehtari, A. 2019. R-squared for Bayesian regression models. *Am. Stat.* **73**: 307–309. doi:[10.1080/00031305.2018.1549100](https://doi.org/10.1080/00031305.2018.1549100).
- Goff, G.P. 1986. Reproductive success of male smallmouth bass in Long Point Bay, Lake Erie. *Trans. Am. Fish. Soc.* **115**(3): 415–423. doi:[10.1577/1548-8659\(1986\)115%3c415:RSOMS%3e2.0.CO;2](https://doi.org/10.1577/1548-8659(1986)115%3c415:RSOMS%3e2.0.CO;2).
- Gravel, M.A., and 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**: 608–616. doi:[10.1111/j.1439-0310.2009.01641.x](https://doi.org/10.1111/j.1439-0310.2009.01641.x).
- Gross, M.R. 2005. The evolution of parental care. *Q. Rev. Biol.* **80**: 37–45. doi:[10.1086/431023](https://doi.org/10.1086/431023). PMID: [15884734](https://pubmed.ncbi.nlm.nih.gov/15884734/).
- Halkka, A., Halkka, L., Halkka, O., Roukka, K., and Pokki, J. 2006. Lagged effects of North Atlantic Oscillation on spittlebug *Philaenus spumarius* (Homoptera) abundance and survival. *Global Change Biol.* **12**: 2250–2262. doi:[10.1111/j.1365-2486.2006.01266.x](https://doi.org/10.1111/j.1365-2486.2006.01266.x).
- Hanson, K.C., Cooke, S.J., Suski, C.D., and Philipp, D.P. 2007. Effects of different angling practices on post-release behaviour of nest-guarding male black bass, *Micropterus* spp. *Fish. Manage. Ecol.* **14**: 141–148. doi:[10.1111/j.1365-2400.2007.00534.x](https://doi.org/10.1111/j.1365-2400.2007.00534.x).
- Hurrell, J.W., Kushnir, Y., Ottersen, G., and Visbeck, M.(eds). 2003. The North Atlantic Oscillation: Climatic Significance and Environmental Impact. *Geophysical Monograph* 134, pp. 1–279.
- Isermann, D.A., Maxwell, J.B., and McInerney, M.C. 2013. Temporal and regional trends in black bass release rates in Minnesota. *North Am. J. Fish. Manage.* **33**: 344–350. doi:[10.1080/02755947.2013.763877](https://doi.org/10.1080/02755947.2013.763877).
- Landsman, S.J., Gingerich, A.J., Philipp, D.P., and Suski, C.D. 2011. The effects of temperature change on the hatching success and larval survival of largemouth bass, *Micropterus salmoides*, and smallmouth bass, *Micropterus dolomieu*. *J. Fish Biol.* **78**: 1200–1212. doi:[10.1111/j.1095-8649.2011.02927.x](https://doi.org/10.1111/j.1095-8649.2011.02927.x). PMID: [21463315](https://pubmed.ncbi.nlm.nih.gov/21463315/).
- Lindenmayer, D.B., Likens, G.E., Andersen, A., Bowman, D., Bull, C.M., Burns, E., et al. 2012. Value of long-term ecological studies. *Aust. Ecol.* **37**: 745–757. doi:[10.1111/j.1442-9993.2011.02351.x](https://doi.org/10.1111/j.1442-9993.2011.02351.x).
- Long, J.M., Allen, M.S., Porak, W.F., and Suski, C.D. 2015. A historical perspective of black bass management in the United States. In *Black bass diversity: multidisciplinary science for conservation*. American Fisheries Society Symposium 82, pp. 99–122.
- Lukas, J.A., and Orth, D.J. 1995. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. *Trans. Am. Fish. Soc.* **124**: 726–735. doi:[10.1577/1548-8659\(1995\)124%3c0726:FANSOS%3e2.3.CO;2](https://doi.org/10.1577/1548-8659(1995)124%3c0726:FANSOS%3e2.3.CO;2).
- MacCrimmon, H.R., and Robbins, W.H. 1975. Distribution of the black basses of North America. In *Black bass biology and management*. Edited by R.H. Stroud and H. Clepper. Sport Fishing Institute, Washington, DC. pp. 56–66.
- Magnuson, J.J. 1990. Long-term ecological research and the invisible present. *BioScience*, **40**: 495–501. doi:[10.2307/1311317](https://doi.org/10.2307/1311317).
- May, R. 1999. Unanswered questions in ecology. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* **354**: 1951–1959. doi:[10.1098/rstb.1999.0534](https://doi.org/10.1098/rstb.1999.0534). PMID: [10670015](https://pubmed.ncbi.nlm.nih.gov/10670015/).
- Myers, R.A. 1998. When do environment–recruitment correlations work? *Rev. Fish Biol. Fish.* **8**: 285–305. doi:[10.1023/A:1008828730759](https://doi.org/10.1023/A:1008828730759).
- Myers, R.A., Taylor, J., Allen, M., and Bonvechio, T.F. 2008. Temporal trends in voluntary release of largemouth bass. *North Am. J. Fish. Manage.* **28**: 428–433. doi:[10.1577/M06-265.1](https://doi.org/10.1577/M06-265.1).
- Neves, R.J. 1975. Factors affecting fry production of smallmouth bass (*Micropterus dolomieu*) in South Branch Lake, Maine. *Trans. Am. Fish. Soc.* **104**(1): 83–87. doi:[10.1577/1548-8659\(1975\)104%3c83:FAPPOS%3e2.0.CO;2](https://doi.org/10.1577/1548-8659(1975)104%3c83:FAPPOS%3e2.0.CO;2).
- Parkos, J.J., and Wahl, D.H. 2002. Towards an understanding of recruitment mechanisms in largemouth bass. In *Black bass: ecology, conservation, and management*. Edited by D.P. Philipp and M.S. Ridgway. American Fisheries Society, Bethesda. pp. 25–45.
- Paukert, C., McInerney, M., and Schultz, R. 2007. Historical trends in creel limits, length-based limits, and season restrictions for black basses in the United States and Canada. *Fisheries*, **32**: 62–72. doi:[10.1577/1548-8446\(2007\)32%5b62:HTICLB%5d2.0.CO;2](https://doi.org/10.1577/1548-8446(2007)32%5b62:HTICLB%5d2.0.CO;2).
- Philipp, D.P., Kaminski, C., and Whitt, G.S. 1985. A comparison of the embryonic development of northern, Florida and reciprocal F1 hybrid largemouth bass in different thermal environments. In *Bulletin of the Illinois Natural History Survey*. pp. 261–273.
- Philipp, D.P., Toline, C.A., Kubacki, M.E., Philipp, D.B.F., and 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. Manage.* **17**: 557–567. doi:[10.1577/1548-8675\(1997\)017%3c0557:TIOCAR%3e2.3.CO;2](https://doi.org/10.1577/1548-8675(1997)017%3c0557:TIOCAR%3e2.3.CO;2).
- Philipp, D.P., Zoldero, A., Lawrence, M.I., Claussen, J.E., Nowell, L., Holder, P., and Cooke, S.J. 2022. COVID-19 reduced recreational fishing effort during the black bass spawning season, resulting in increases in black bass reproductive success and annual recruitment. *Fish. Res.* **259**: 106580.
- Quinn, S. 2002. Status of seasonal restrictions on black bass fisheries in Canada and the United States. In *Black bass: ecology, conservation, and management*. Edited by D.P. Philipp and M.S. Ridgway. American Fisheries Society, Bethesda. pp. 455–465.
- Quinn, S., and Paukert, C. 2009. Centrarchid fisheries. In *Centrarchid fishes: diversity, biology, and conservation*. Edited by S. Cooke and D.P. Philipp. Wiley-Blackwell. pp. 312–339.
- Raffetto, N.S., Baylis, J.R., and Serns, S.L. 1990. Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus dolomieu*). *Ecology*, **71**: 1523–1535. doi:[10.2307/1938289](https://doi.org/10.2307/1938289).
- Ridgway, M.S., and Friesen, T.G. 1992. Annual variation in parental care in smallmouth bass, *Micropterus dolomieu*. *Environ. Biol. Fishes.* **35**: 243–255. doi:[10.1007/BF00001890](https://doi.org/10.1007/BF00001890).
- Ridgway, M.S., Goff, G.P., and Keenleyside, M.H.A. 1989. Courtship and spawning behavior in smallmouth bass (*Micropterus dolomieu*). *Am. Midl. Nat.* **122**: 209–213. doi:[10.2307/2425905](https://doi.org/10.2307/2425905).
- Ridgway, M.S., Shuter, B.J., and Post, E.E. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). *J. Anim. Ecol.* **60**: 665–681. doi:[10.2307/5304](https://doi.org/10.2307/5304).
- Rogers, M.W., and Allen, M.S. 2009. Exploring the generality of recruitment hypotheses for largemouth bass along a latitudinal gradient of Florida lakes. *Trans. Am. Fish. Soc.* **138**: 23–37. doi:[10.1577/T07-178.1](https://doi.org/10.1577/T07-178.1).
- Scott, W., and Crossman, E.J. 1973. *Freshwater fishes of Canada*. Canada Fisheries Research Bulletin, Ottawa.
- Serns, S.L. 1982. Relation of temperature and population density to first-year recruitment and growth of smallmouth bass in a Wisconsin lake. *Trans. Am. Fish. Soc.* **111**: 570–574. doi:[10.1577/1548-8659\(1982\)111%3c570:ROTAPD%3e2.0.CO;2](https://doi.org/10.1577/1548-8659(1982)111%3c570:ROTAPD%3e2.0.CO;2).
- Shaw, S.L., and Allen, M.S. 2014. Localized spatial and temporal variation in reproductive effort of Florida bass. *Trans. Am. Fish. Soc.* **143**: 85–96. doi:[10.1080/00028487.2013.829123](https://doi.org/10.1080/00028487.2013.829123).

- Shaw, S.L., and Allen, M.S. 2016. Quantifying recruitment compensation in Florida largemouth bass, with implications for fisheries. *Trans. Am. Fish. Soc.* **145**: 462–475. doi:10.1080/00028487.2015.1131744.
- Shuter, B., Maclean, J.A., Fry, F.E.J., and Regier, H.A. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Trans. Am. Fish. Soc.* **109**: 1–34. doi:10.1577/1548-8659(1980)109%3c1:SSOTEO%3e2.0.CO;2.
- Shuter, B.J., and Ridgway, M.S. 2002. Bass in time and space: operational definitions of risk. In *Proceedings of the American Fisheries Society Symposium* 31. pp. 235–249.
- Stan Development Team. 2017. Stan modeling language: user's guide and reference manual. Version 2.17. 0. Available from <http://mc-stan.org> [accessed August 2022].
- Stein, J.A., and Philipp, D.P. 2015. Quantifying brood predation in largemouth bass (*Micropterus salmoides*) associated with catch-and-release angling of nesting males. *Environ. Biol. Fishes*, **98**: 145–154. doi:10.1007/s10641-014-0244-9.
- Steinhart, G.B., Dunlop, E.S., Ridgway, M.S., and Marschall, E.A. 2008. Should I stay or should I go? Optimal parental care decisions of a nest-guarding fish. *Evol. Ecol. Res.* **10**: 351–371.
- Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K-S., et al. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. R. Soc. Lond. B*, **270**: 2087–2096. doi:10.1098/rspb.2003.2415.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K-S., and Lima, M. 2002. Ecological effects of climate fluctuations. *Science*, **297**: 1292–1296. doi:10.1126/science.1071281. PMID: 12193777.
- Straille, D., Livingstone, D.M., Weyhenmeyer, G.A., and George, D.G. 2003. The response of freshwater ecosystems to climate variability associated with the North Atlantic Oscillation. In *The North Atlantic Oscillation: climate significance and environmental impact*. Edited by J.W. Hurrell, Y. Kushnir, G. Ottersen and M. Visbeck. American Geophysical Union. pp. 263–279.
- Suski, C.D., and Philipp, D.P. 2004. Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. *Trans. Am. Fish. Soc.* **133**: 1100–1106. doi:10.1577/T03-079.1.
- Suski, C.D., and Ridgway, M.S. 2007. Climate and body size influence nest survival in a fish with parental care. *J. Anim. Ecol.* **76**: 730–739. doi:10.1111/j.1365-2656.2007.01242.x. PMID: 17584379.
- Suski, C.D., Svec, J.H., Ludden, J.B., Phelan, F.S., and Philipp, D.P. 2003. The effect of catch-and-release angling on the parental care behavior of male smallmouth bass. *Trans. Am. Fish. Soc.* **132**: 210–218. doi:10.1577/1548-8659(2003)132%3c0210:TEOCAR%3e2.0.CO;2.
- Sutter, D.A.H., Shaw, S.L., Allen, M.S., Philipp, D.P., and Suski, C.D. 2014. Reproductive investment drives capture probability in fish: an interspecific comparison. *Fish. Manage. Ecol.* **21**: 338–342. doi:10.1111/fme.12073.
- Trippel, N.A., Hargrove, J.S., Leone, E.H., Austin, J.D., and Allen, M.S. 2017. Angling-induced impacts on recruitment and contributions to reproduction in Florida bass. *Trans. Am. Fish. Soc.* **146**: 871–887. doi:10.1080/00028487.2017.1301997.
- Vehtari, A., Gelman, A.E., and Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**: 1413–1432. doi:10.1007/s11222-016-9696-4.
- Wagner, T., Jubar, A.K., and Bremigan, M.T. 2006. Can habitat alteration and spring angling explain largemouth bass nest success? *Trans. Am. Fish. Soc.* **135**(4): 843–852. doi:10.1577/T05-198.1.
- Walters, C.J., and Martell, S. 2004. *Fisheries ecology and management*. Princeton University Press, Princeton, NJ, USA. 381p.
- Wan, X., Holyoak, M., Yan, C., Le Maho, Y., Dirzo, R., Krebs, C.J., et al. 2022. Broad-scale climate variation drives the dynamics of animal populations: a global multi-taxa analysis. *Biol. Rev.* **97**: 2174–2194. doi:10.1111/brv.12888. PMID: 35942895.
- Watt, K.E.F. 1959. Studies on population productivity II. Factors governing productivity in a population of smallmouth bass. *Ecol. Monogr.* **29**: 367–392. doi:10.2307/1942135.
- Weatherhead, P.J. 1986. How unusual are unusual events? *Am. Nat.* **128**: 150–154. doi:10.1086/284550 10.1086/284550.
- Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**(916): 687–690. doi:10.1086/282461.
- Wydoski, R.S. 1977. Relation of hooking mortality and sublethal hooking stress to quality fishery management: catch-and-release fishing as a management tool. Humboldt State University, Arcata, CA.
- Zipkin, E.F., Gardner, B., Gilbert, A.T., O'Connell, A.F., Royle, J.A., and Silverman, E.D. 2010. Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics. *Oecologia*, **183**: 893–902. doi:10.1007/s00442-010-1622-4.
- Zuckerman, Z., and Suski, C. 2013. Predator burden and past investment affect brood abandonment decisions in a parental care-providing teleost. *Funct. Ecol.* **27**(3): 693–701. doi:10.1111/1365-2435.12074.
- Zuckerman, Z.C., Philipp, D.P., and Suski, C.D. 2014. The influence of brood loss on nest abandonment decisions in largemouth bass *Micropterus salmoides*. *J. Fish Biol.* **84**: 1863–1875. doi:10.1111/jfb.12404. PMID: 24890406.