Size-associated energetic constraints on the seasonal onset of reproduction in a species with indeterminate growth

ABSTRACT

The seasonal onset of reproduction is constrained in many systems by a need to first accumulate energetic reserves. Consequently, the observation that larger individuals reproduce earlier may be due to a negative relationship between size and mass-specific basal metabolic rate that is shared across diverse taxa. However, an untested prediction of this hypothesis is that individuals should be metabolically efficient enough to escape energetic constraints above a certain size threshold. Seasonally reproducing species, such as temperate fishes, that must recover winter energy losses before reproduction and exhibit indeterminate growth are ideal models to test this prediction. We harness decade-long behavioral data on parental male smallmouth bass, *Micropterus dolomieu,* to investigate contributions of energetic allometry to differences in reproductive timing. At the population level, peak seasonal reproductive timing (i.e., the median date on which eggs were found in nests each year) was negatively related to degree days–a measure of thermal energy experienced–before reproduction. At the individual level, degree days accumulated by males before reproduction was related to male size and condition in every year, but the impact of temperature on reproductive timing by the largest males was relaxed in most years. Additionally, we used our data to replicate the analyses of two previous studies of *M. dolomieu* populations and found virtually identical negative associations between male body size and degree days accumulated before reproduction. Our results suggest that in smallmouth bass the onset of seasonal reproduction is constrained by basal metabolic rate–as indicated by total length–and that large individuals can escape size-associated energetic constraints. We reveal a more complicated relationship between size and reproductive timing than earlier studies, which may be relevant for many species. Knowledge of this relationship is critical to understanding how a changing climate will influence population dynamics of economically, ecologically, and recreationally important species like *M. dolomieu*.

Key words: **allometry, body size, Centrarchidae, degree days, metabolism, phenology, reproductive timing, temperature**

INTRODUCTION

Reproductive phenology can have considerable consequences for fitness (Cargnelli and Gross 1996; Post et al. 1998; Post 2003) and is influenced by energetic constraints across a diverse set of taxa, including amphibians, fishes, mammals, and birds (Jørgensen 1982; Danylchuk and Fox 1994; Dobson and Michener 1995; Descamps et al. 2011). The use of proportionately less energy by larger individuals has also been documented across a diverse set of taxa (i.e., they show a negative allometric relationship between body size and mass-specific basal metabolic rate; Kleiber 1947; Lasiewski and Dawson 1967; Cargnelli and Gross 1997; West et al. 1997; Clarke and Johnston 1999; Hurst and Conover 2003; Nagy 2005; Blanckenhorn et al. 2007; Makarieva et al. 2008; Brodeur et al. 2020). Hence, the common observation that larger individuals reproduce before smaller individuals is often attributed to energetic costs that constrain the initiation of reproduction (Tejedo 1992; Danylchuk and Fox 1994; Dobson and Michener 1995; Descamps et al. 2011). This relationship between size and reproductive timing is especially prominent in species with high reproductive costs resulting from, e.g., energetically costly gametes or parental care behavior, including nest construction and defense (Ridgway et al. 1991; Tejedo 1992; Danylchuk and Fox 1994; Descamps et al. 2011). The presence of species–specific constants in models of allometric scaling laws leads us to expect similar associations between body size and reproductive timing across different populations if energetics control behavior (West et al. 1997).

Often, the relationship between size and reproductive timing is described by a linear function or even more simply as a correlation (Tejedo 1992; Danylchuk and Fox

1994; Dobson and Michener 1995; Descamps et al. 2011). However, if energetic costs constrain the onset of seasonal reproduction and metabolic efficiency scales positively with size, we predict that above a certain size, individuals could be metabolically efficient enough to initiate reproduction without any delay attributable to the recovery of energetic reserves that have been lost over winter; that is, the relationship between reproductive timing and size should be curvilinear, with a diminished association at larger body sizes. Indeed, log-log or log-untransformed linear regression models that describe a negative relationship between size and reproductive timing imply that the relationship is non-linear, where the effect of energetic constraints is reduced amongst larger individuals (e.g., Ridgway et al. 1991, Wiegmann et al., 1992; Lukas and Orth 1995). In some circumstances, we anticipate large individuals could be unconstrained metabolically and a quadratic function might better describe the relationship between (log-transformed) measures of size and reproductive phenology, where the size threshold at which individuals are released from metabolic constraints may depend on environmental conditions that control the gain or loss of energetic reserves.

In fishes, indeterminate growth can lead to substantial variation in size among mature adults (Ridgway and Friesen 1992; Knapp et al. 1996; Wiegmann et al. 1997; Dickerson et al. 2005). This situation provides ideal conditions to test the hypothesis that the impact of energetic constraints on reproductive phenology is size dependent. In some species, within-season variation in timing of reproduction is known to have large fitness consequences (Cargnelli and Gross 1996; Post et al. 1998; Post 2003), and in some fishes, a negative allometric relationship to mass-specific basal metabolism has been implicated (Shuter and Post 1990; Cargnelli and Gross 1997; Clarke and Johnston

1999). In north-temperate fishes, where males of many species rely almost entirely on stored energy reserves throughout winter (Shuter and Post 1990), a negative allometric relationship could explain why larger males, which lose proportionately less of their winter energy reserves than smaller males, spawn earlier in a season (Post and Evans 1989; Ridgway et al. 1991; Fullerton et al. 2000). In freshwater fishes like these, individual thermal history can have a substantial impact on energetic stores and the ability of individuals to recoup winter energy losses. Changing climate makes studies investigating relationships between temperature and reproductive phenology particularly important.

Here, we use a long-term dataset on an economically and ecologically important species, smallmouth bass, *Micropterus dolomieu*, (Carey et al., 2011; Kim et al., 2022) to test the influence of energetics on reproductive timing. In particular, we followed the reproductive behavior of individual males in a closed population over 10 reproductive seasons to investigate how male body size, condition, and thermal history impact reproductive timing. In northern populations, *M. dolomieu* are dormant in winter and resume activity when water temperatures reach 10 ºC, after which males build nests and defend progeny until they disperse (Shuter et al., 1980; Hinch and Collins 1991). Parental males consume little over the care period and there is good evidence that implicates energetics as the primary driver of *M. dolomieu* reproductive timing (Ridgway et al. 1991; Ridgway and Shuter 1994; Gillooly and Baylis 1999; Mackereth et al. 1999). Hence, the distribution of reproductive dates of the population is expected to be sensitive to temperature patterns in early spring that control the rate at which males are able to recoup winter energy losses and reach some threshold energetic reserve that is sufficient to carry them through the nest-guarding period.

In this study, we consider how reproductive timing of the population as a whole responds to the rise of spring water temperature and test the hypothesis that timing of peak reproduction is negatively related to the number of degree days–a measure of the thermal energy experienced by an individual–accumulated before the water temperature reaches 15 °C, the temperature threshold associated with the initiation of reproduction in many smallmouth bass populations (Hubbs and Bailey 1938; Shuter et al. 1980). Next, we examine the linear relationship between total body length and the degree days males accumulated before they spawned and compare the slope of this relationship to slopes acquired from two other *M. dolomieu* populations (Ridgway et al. 1991; Lukas and Orth, 1995). Finally, we test the prediction, not addressed in prior studies, that there is a size threshold at which the energetic constraint on the seasonal onset of reproduction is relaxed, and explore whether incorporating body condition into our analysis improves our ability to predict reproductive timing.

Study system natural history

Smallmouth bass, *Micropterus dolomieu*, are native to North America and reproduce seasonally, when water temperatures approach 15 ºC (Hubbs and Bailey 1938; Shuter et al. 1980). Males construct nests in the littoral zone, where females deposit eggs. Typically, males mate with only one female and no sneaker behavior has been reported (Ridgway 1989; Raffetto et al. 1990; Wiegmann et al. 1992). Recent genetic work by Franckowiak et al. (2017) suggests, however, that nests of a small percentage of males contain eggs from multiple females. After spawning, males remain in close proximity to their nest and defend offspring until their fry swim up and disperse, a period that may last several weeks (Hinch and Collins 1991). Parental behavior is costly and leads to a net loss of lean mass, as males rarely feed during this period (Gillooly and Baylis 1999). In northern populations, smallmouth bass activity ceases when water temperatures drop below 10 ºC, and over winter individuals are largely dormant, consume little food and engage in limited movement (Hubbs and Bailey 1938; Munther 1970; Oliver et al. 1979; but see Lyons and Kanehl 2002; Schreer and Cooke 2002). The energetic cost of parental care in combination with the fact that smaller males may end winter with a proportionately larger energy deficit than larger males may explain the observation that larger males spawn earlier within a season than smaller males, as suggested by the relationships between size and reproductive timing found by Ridgway et al. (1991) and Lukas and Orth (1995).

MATERIALS AND METHODS

Study site

We conducted this study in 1999 and 2001-2009 on Pallette Lake, a 70-ha research lake in the Northern Highlands Fishery Research Area of north-central Wisconsin (46.067° N/89.604° W). The Wisconsin Department of Natural Resources manages this lake, which is closed to fish migration and has a maximum depth of approximately 20 m and a mean depth of approximately 10 m. Saunders et al. (2002) describe the benthic and limnological characteristics of the lake in detail. Anglers are subject to a mandatory creel census, where caught fish must be reported to ensure regulations are followed. From 1999-2006, regulations required anglers to return to the lake any male less than 41 cm total length and from 2007 onwards all males under 51 cm had to be returned. We had significant representation of males larger than 40 cm in our analyses (13.8%).

Annual nest census

We initiated surveys each year when the water temperature approached 15 °C, typically in mid to late May, and continued until males ceased nest construction (late June to early July) and progeny in most nests had dispersed. Two to three crew members with snorkels searched for nests as they swam transects running from the shoreline out to a depth of about 4 m. This depth was well beyond both the average 1.7 m depth at which nests in the lake were found and the maximum depth of smallmouth bass nests found in studies of other Wisconsin lakes (Bozek et al. 2002). When each nest was discovered, snorkelers placed a numbered tag constructed from a strip of Rite-n-Rain paper tied to a sinker on the edge of the nest and recorded the date, stage of embryos (if present), depth, location and distinctive landmarks that might be useful to relocate nests.

Characteristics of parental males

We captured parental males from their nests with hand nets and recorded their total length (cm) and weight (g). Each male was marked with a uniquely numbered Floy FD-67C anchor tag (University of Wisconsin RARC protocol A-48-9700-L00173-2-04-99). These tags allowed us to track individuals across seasons and estimate the total number of males that spawned each year, although analyses on reproductive timing were limited to those males that were found with eggs in their nest to ensure estimates of degree days before reproduction were comparable across individuals (Table 1).

Temperature and degree days

We used temperature data to estimate the thermal energy experienced by males in each year. A thermograph positioned near the shoreline at an approximate depth of 1 m recorded the water temperature (°C) hourly when the lake was not covered by ice. Thermograph malfunctions or other disturbances (e.g., removal of the thermograph from the lake by a lake visitor) resulted in some missing temperature records over the 10 years. We estimated these records using regression equations that characterized the relationship between water temperature in our study site (Pallette Lake) and nearby Sparkling Lake (46.010° N/89.701° W), a North Temperate Lakes Long-Term Ecological Research lake (64 ha; maximum depth 20 m) that has a nearly identical temperature profile as Pallette Lake (range of adjusted R^2 over the 10-year study: 0.87 – 0.99; $P < 0.0001$; Supplementary Figure S1 and Table S1).

These temperature data were used to compute degree days, a measure of the thermal energy experienced by individuals (Chezik et al. 2014a, b). In particular, we used the sum of positive differences between the average daily water temperature at 1 m and the threshold $T_0 = 10$ °C for each day until the date that the average water temperature reached 15 ºC, the temperature at which seasonal reproductive activity is typically initiated, to evaluate the population-level reproduction response to temperature each year (Shuter et al. 1980; Ridgway et al. 1991; Lukas and Orth 1995). The sum of degree days each year from the first date on which the water temperature was favorable for energy recuperation (i.e., average exceeded 10 °C) until the date at which eggs were found in the nest of a male was also computed to produce a measure of the seasonal thermal energy experienced by each parental male prior to reproduction and evaluate individual responses to temperature (Shuter et al. 1980; Ridgway et al. 1991). In addition, we calculated the average and maximum temperature of the growth season for every year, defined as the period between the first day the average temperature climbed above 10 ºC and the last day before the average temperature dropped below 10 ºC, and the duration of winter, defined as the number of days between growth seasons (Shuter et al., 1980; Ridgway et al., 1991; Table 1). These latter measures of thermal energy were used to explore how temperature may control a size threshold at which males are released from energetic constraints on seasonal reproductive phenology.

Statistical analyses

Estimating body condition

Individual condition, often measured as some function of body mass, may provide an estimate of energetic reserves for individuals of a specified size and, hence, influence reproductive phenology (Kaufman et al. 2007, Schloesser and Fabrizio 2017). Individual condition was calculated as the residual of the relationship between weight (natural log [ln] transformed) and length (ln transformed) for each year, which has been shown to successfully predict energy content in a broad set of fish species (Kaufman et al. 2007, Schloesser and Fabrizio 2017).

Population-level responses to thermal energy

We used linear regression to predict annual population response times, the time interval between the date on which the mean water temperature reached 15 ºC and the median date on which eggs were found in nests, from the number of degree days accumulated before the first 15 ºC day each year. If thermal energy controls individual reproductive readiness, then we expect the slope of this relationship to be negative (Shuter et al. 1980).

Individual behavioral response to thermal energy

We first used a linear mixed model structured similarly to those used in prior studies on smallmouth bass reproductive timing, where size was regressed on reproductive timing and year, to generate a comparable measure of the relationship between male total length (ln transformed) and the number of degree days (ln transformed, threshold $T_0 = 10$ °C) that had accumulated up to the date on which a male spawned (i.e., the date a nest was found to contain eggs) (Ridgway et al. 1991; Lukas and Orth, 1995). Individual identifiers were included as a random effect because 316 individuals bred in more than one season. If a temperature-dependent metabolic process is the main driver of reproductive timing, species–specific constants in allometric scaling laws predict the slopes of these relationships to be similar across studies (West et al. 1997).

Next, to examine predictions related to the presence of an energetic threshold and to explore whether incorporating condition improves predictions of reproductive timing, we fit and competed a set of models predicting the degree days a male accumulated prior to reproduction. Alternative models included as predictors all combinations of condition, length (ln transformed), and length^2 (ln transformed), which allowed the effect of body size on reproductive timing to vary. Indicators for years and a random effect for individuals were included in all models. Models were tested with and without year interactions with condition or the two body length terms. Akaike information criterion (AIC) was used to choose between models (Akaike 1973). Some males spawned more than once within a season (N=127). In these cases, we restricted the analysis to the first attempt within a year. We excluded data from approximately one third of males (34.6%) whose nests were discovered after eggs had hatched, because timing of reproduction could not be definitively determined for these males. The mean size and range of sizes of these males was qualitatively very similar to those included in the study so we did not expect this to bias our results. If larger males experience less severe winter energy losses, then the slope of the relationship between male length and degree days accumulated before reproduction is expected to be negative in each year (Ridgway et al. 1991). If there is a size threshold above which males can escape energetic constraints on reproduction, we expected the quadratic length term to be included in the chosen model. Similar models including condition, length (ln transformed), and length^2 (ln transformed) as predictors of reproductive timing were conducted for each year independently to validate results of our comprehensive model (Supplement; Supplementary Table S3).

Post hoc linear models were conducted to test the hypothesis that in years where environmental conditions favored the accumulation of greater energetic reserves, energetic constraints on reproduction should be restricted to smaller individuals (Supplementary Table S4). Specifically, we investigated the relationship between the size threshold at which there was no relationship between size and degree days before reproduction in a given year–given by the untransformed body length of the parabolic vertex in the best regression models–and environmental variables that we hypothesized might influence the size threshold at which individuals are released from metabolic constraints (Supplementary Table S4). These environmental variables included the degree days accumulated before 15 ºC, the duration (days) of the winter, the duration (days) of the previous season, the number of degree days accumulated during the previous growth season, and the average temperature of the previous growth season.

RESULTS

Characteristics of parental males and seasonal temperature variation

Males were caught from 2,055 nests throughout the course of the 10-year study, and 847 unique males were tagged. On average, we failed to capture ~5% of parental males from nests discovered to contain eggs or more advanced progeny per year throughout the course of the study. The majority of these instances occurred when offspring died and the nest was abandoned before a male was captured. The number of males on nests each year ranged from 102 to 284, and the nests of 88 to 159 of these individuals contained eggs when they were discovered. The total length of males with known spawn dates ranged from 17 cm to 47.5 cm (N = 1261), and the seasonal average ranged from 30.3 ± 0.7 to 35.4 ± 0.5 cm across years. Temperature patterns also varied yearly. The duration of winter ranged from 174 days before the 2001 growth season to 211 days before the 2002 growth season. The mean temperature of the growth season ranged from 17.4 to 20.1 ºC (Table 1).

Responses to thermal energy

Population-level responses

The dates on which peak reproduction occurred (i.e., the median date on which eggs were found in nests each year) ranged from 23 May in 2001 to 10 June in 2004. The degree days accumulated before the first day that temperatures reached an average of 15 ºC varied greatly between years–from 13.1 in 2002 to 77.3 in 2009 (Table 1). In years where more degree days were accumulated before the first 15 ºC day, the population-level response time was shorter ($N = 10$, $R^2 = 0.46$, $P = 0.02$; Figure 1). Indeed, in 2009 peak reproduction actually occurred 3 days before the first day that water temperature reached an average of 15 ºC.

Individual behavior

A linear mixed model revealed a negative linear relationship between male total length (ln transformed) and the degree days (ln transformed) a male accumulated prior to reproduction in all ten years of the study ($N = 1261$, $R^2 = 0.67$, $P < 0.0001$; Supplement; Supplementary Figure S2). The coefficient that described the relationship between size and degree days before reproduction was $b = -0.375 \pm 0.011$ ($P < 0.0001$).

A comparison of models predicting the degree days a male accumulated prior to reproduction revealed a single best model, with an AIC weight of 0.83. This model included a linear and quadratic term for male total length (ln transformed), an interaction term between each length term and year, and an effect of condition that was independent of year ($N = 1261$, $R^2 = 0.67$; Figure 2, Table S2). The linear coefficient associated with body size was strongly negative and the quadratic term was positive in every year except for 1999 (mean = -9.183 ± 8.5, range = -26.44 to 3.94; mean = 1.15 ±

1.2, range = -0.73 to 3.59 respectively). Hence, the effect of body size on reproductive timing was generally reduced amongst larger individuals. The effect of condition on degree days accumulated before reproduction was -0.33 (95% CI: -0.49, -0.17). None of the environmental variables tested in *post hoc* models significantly predicted the size threshold for energetic constraints (Supplementary Table S4).

DISCUSSION

Reproductive timing has important fitness consequences (Cargnelli and Gross 1996; Post et al. 1998; Post 2003) and is related to size-associated energetic constraints in many animals (Tejedo 1992; Danylchuk and Fox 1994; Dobson and Michener 1995; Descamps et al. 2011). The patterns observed in this 10-year study at both the population and individual level suggest that reproductive timing by male *M. dolomieu* in Pallette Lake is driven by energetic constraints, where the magnitude of the constraint varies amongst individuals of different sizes.

Population level responses

The delay between the temperature threshold associated with the initiation of smallmouth bass reproduction (15 ºC) and the date of peak reproduction was shorter in years where more degree days accumulated prior to the temperature threshold, as observed in an earlier study (Figure 1, Shuter et al. 1980). Higher thermal energy experienced by the population in early spring appears to push the peak seasonal distribution of reproduction dates earlier, presumably because males of all sizes are able to recoup winter energy losses and reach some threshold energetic reserve that is sufficient to carry them through the parental period. The pattern likely also depends on female reproductive phenology, which has been little studied but based on spring activity and egg deposition patterns appears to be similarly driven by an association between body size and temperature (Ridgway et al. 1991; Wiegmann et al. 1992; Franckowiak et al., 2017). Population responses to temperature may be particularly important for the prediction of future *M. dolomieu* reproductive patterns given that North American temperate lakes like ours have experienced increases in winter and spring temperatures in the past 35 years associated with advances in other biologically relevant phenomena like ice melt (Hewitt et al. 2018).

Similarities across smallmouth bass populations

Ridgway et al. (1991) and Lukas and Orth (1995) examined the association between male total length and degree days accumulated prior to reproduction in Opeongo Lake, Nipissing District, Ontario and North Anna River, Virginia, over six years and one year, respectively. In these studies, male length was regressed on degree days (both ln transformed) and Lukas and Orth (1995) noted the similarity of the slopes between the two studies: -0.355 and -0.391. The analysis conducted by Ridgway et al. (1991) indicated that the slope of the relationship did not differ significantly across years.

We conducted an equivalent regression analysis with our data and found a slope of -0.375 across all years, which is remarkably similar to those found in these two earlier studies (Figure S2). The similarity of slopes that characterize the relationship between male body size and accumulated degree days prior to reproduction in three geographically distinct smallmouth bass systems suggests that reproductive timing is controlled by a conserved metabolic pathway and that a single parameterization based on physiological time—that is, accumulated thermal energy—may control reproductive timing in diverse systems.

Size threshold for energetic constraints

Here, we identify a novel relationship between size and reproductive timing that reflects a differential role of energetic constraints on reproduction in individuals of varying sizes. Assertions that negative allometric relationships with mass specific basal metabolic rate are what allow larger individuals to reproduce earlier in a season (Tejedo 1992; Danylchuk and Fox 1994; Dobson and Michener 1995; Descamps et al. 2011) allow for a logical untested prediction: Individuals should be metabolically efficient enough to escape energetic constraints on the seasonal onset of reproduction altogether above a certain size threshold. Indeed, in our population, we found that models with a quadratic length term better explained variation in the timing of reproduction than linear models like those produced by prior studies on smallmouth bass (Ridgway et al. 1991; Lukas and Orth 1995). While the magnitude of the quadratic length term varied across years, it was positive in 9 out of the ten years of our study, which is consistent with the relaxation of energetic constraints on the reproductive timing of larger individuals.

The inverse curvature of the relationship between size and reproductive timing in 1999 appears to be driven by 11 males that were shorter than 25 cm and among the smallest individuals to reproduce across all years. Reproduction by these males corresponded to a mid-season drop in the average daily temperature to below 15 ºC and a subsequent raise to over 19 ºC. The 15 ºC temperature threshold, which usually marks the start of a reproductive season, likely induced these males, now with recouped energy reserves, to adopt a potentially maladaptive decision and spawn despite the actual short amount of time left in the season. Indeed, studies have found that smallmouth bass fitness is lowest in small parents that reproduce late in the season (Shuter 1980; Wiegmann et al. 1992; Suski and Ridgway 2007).

Any environmental factors that influence metabolism or overall energetic reserves of individuals may have been responsible for the differences in size threshold across the years of this study. For example, if the winter preceding reproduction is longer, we would expect a higher size threshold for males to be energetically efficient enough to escape the need to recuperate energetic losses before reproducing. Further, if the preceding growth season (when temperatures are above 10º C) is shorter, or there are few degree days accumulated at the start of a season before the reproductive temperature threshold associated with the start of smallmouth bass reproduction occurs, this could lead to a similar result. However, we found no specific evidence in our study of associations between these or other measures of temperature variability and differences in size threshold across years (Table S4). Other environmental variables that were not measured here, notably food availability, can influence energetic reserves and reproduction in smallmouth bass as well and may explain additional interannual variation or the lack of a relationship between interannual temperature regimes and the curvature of the slope between size and reproductive timing (Ridgway and Shuter 1994).

The role of condition

The influence of condition on reproductive timing may be more pronounced in species with determinate growth, where truncated size of sexually mature adults limits variation in size-associated differences in metabolic rate (Dobson and Michener 1995). In our study, condition was included in our top-ranked model, indicating that this feature of males improved the model fit, but the biological effect appeared to be minor. The difference in reproductive timing between males in the 95th and 5th percentiles of condition was minimal (mean = 1.09 degree days ± 0.01, range = 1.07 to 1.11; see Figure 2). This supports our expectation that, when growth is indeterminant and there are large differences of body size amongst adults, differences in basal metabolic rate–as indicated by total length–should have a stronger impact on timing of reproduction than differences in individual condition, which may be brought about by stochastic environmental or ecological factors such as recent feeding success. Even in some species with determinate growth, such as arctic seabirds, early empirical evidence has shown that with body condition accounted for, individual rate of energetic gain is the major predictor of breeding phenology (Hennin et al., 2016). Thus, the broad significance of metabolic rate in determining timing of reproduction in species where reproduction is constrained by the accumulation of energetic reserves may explain the outsized importance of length relative to body condition found in this study.

Alternative hypotheses

Recent research has suggested that metabolic scaling in metazoans is predicted by the optimization of growth and reproduction to maximize lifetime reproductive success (White et al. 2022). This raises a number of alternative hypotheses which may explain the patterns of size–associated reproductive timing observed in this study. In particular, there may be some adaptive benefit to smaller males reproducing later in the season, either because conditions are more favorable to their reproduction, or their offspring would gain some advantage from the different temperature environment. One potential benefit to delaying reproduction may be avoiding competition with larger males who reproduce earlier in the season. However, Ridgway et al., (1991) removed large males from a lake population and saw no advancement of reproductive timing among smaller males. Another benefit to delaying reproduction is that less energy may be expended by late reproducers because warmer temperatures later in the season lead to faster maturing fry, which require fewer days of parental care (Ridgway and Friesen, 1992). However, this does not preclude the possibility that patterns of reproductive timing are driven by size-associated differences in energy deficits after winter. Smaller males may end winter with proportionately larger energy deficits and require more time to recuperate energy reserves before reproduction in addition to benefiting from the lower energy requirements of late season parental care. Further, in smallmouth bass, individuals who reproduce late in the season are known to obtain fewer eggs (Ridgway and Friesen, 1992) and produce offspring who are smaller at the onset of winter and have lower survival rates (Oliver et al., 1979; Shuter et al., 1980). Thus, there are many fitness consequences to delaying reproduction which stand contrary to the idea that smaller individuals delay reproduction only to gain an adaptive advantage and not because their reproductive onset is constrained by metabolic factors associated with size.

Applications for management and conservation

In addition to being ecologically relevant as a damaging invasive species, smallmouth bass are one of the world’s most popular species for recreational fishing and are responsible for hundreds of millions of dollars of retail sales, wages, and tax revenue in the United States alone each year (Carey et al., 2011; Kim et al., 2022). They have a history of management that stretches back nearly 200 years and the identification of novel relationships between individual phenotype and reproduction may support current efforts focused on the restoration of native populations (Long et al. 2015). In other high latitude North American fishes that experience cold winters, similar relationships between temperature, size and reproductive timing also likely apply (e.g., Cargnelli and Gross 1997; Hurst and Conover 2003). Changing climate conditions have the potential to disrupt the dynamics of reproductive timing, and higher latitude freshwater fish communities are particularly vulnerable to these changes (Visser and Both 2005; Todd et al. 2011; Shuter et al. 2012; Hovel et al. 2017). For example, shorter, less severe winters could relax energetic constraints on smaller individuals and induce a change in control of the onset of seasonal reproduction from one based on the time it takes to become energetically prepared to construct and defend a nest to one more dependent on other ecological factors such as male competitive status, or female mate choice. Because the transfer of thermal heat from the environment to fishes accumulates with time, even small changes in temperature through development could cause significant differences in growth trajectories over the life of an individual (Neuheimer and Taggart 2007). Further studies that address how energetic constraints differentially influence phenology and depend on individual phenotype, as well as possible differences between the sexes, will be critical to understanding how population dynamics will change as temperatures continue to shift across the globe. Specifically, the results presented here demonstrate that investigations of reproductive timing may benefit from distinguishing between individuals of different sizes that may experience differential environmental constraints, particularly in species with indeterminate growth.

Conclusions

Across diverse species, size and, in particular, size thresholds, play an important role in determining individual phenotype through ontogeny, control of alternative reproductive tactics, life history decision making, diet shifts and more (Thomas and Ickes 1995; Piché et al. 2008; Lucifora et al. 2009; Smallegange 2010; Yasuno et al. 2012; Wilmes et al. 2020). In this study we identify a novel pattern of size-associated reproductive timing and provide further support of an underlying energetic mechanism. Our results suggest the existence of a biological size threshold at which energetic constraints on reproductive phenology are relaxed, a threshold that may become more relevant as global temperatures increase and more individuals are able to escape the energetic constraints that currently dictate their behavior.

REFERENCES

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. Proceedings of the 2nd international symposium on information theory. Second Int Symp Inf Theory.

Alcock J. 1994. Body size and its effect on male-male competition in *Hylaeus alcyoneus* (Hymenoptera: Colletidae). J Insect Behav. Doi:10.1007/BF01988901.

Angiulli E, Pagliara V, Cioni C, Frabetti F, Pizzetti F, Alleva E, Toni M. 2020. Increase in environmental temperature affects exploratory behaviour, anxiety and social preference in *Danio rerio*. Sci Rep. doi:10.1038/s41598-020-62331-1.

Baylis JR, Wiegmann DD, Hoff MH. 1993. Alternating life histories of smallmouth bass. Trans Am Fish Soc. Doi:10.1577/1548-8659(1993)122<0500:alhosb>2.3.co;2.

Biro PA, Beckmann C, Stamps JA. 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. Proc R Soc B Biol Sci. doi:10.1098/rspb.2009.1346.

Blanckenhorn WU, Fanti J, Reim C. 2007. Size-dependent energy reserves, energy utilization and longevity in the yellow dung fly. Physiol Entomol. Doi:10.1111/j.1365-3032.2007.00589.x.

Boesch C, Kohou G, Néné H, Vigilant L. 2006. Male competition and paternity in wild chimpanzees of the Taï forest. Am J Phys Anthropol. Doi:10.1002/ajpa.20341.

Bozek MA, Short PH, Edwards CJ, Jennings MJ, Newman SP. 2002. Habitat selection of nesting smallmouth bass *Micropterus dolomieu* in two north temperate lakes. Am Fish Soc Symp. 31:135-148.

Brandão ML, Colognesi G, Bolognesi MC, Costa-Ferreira RS, Carvalho TB, Gonçalves-de-Freitas E. 2018. Water temperature affects aggressive interactions in a Neotropical cichlid fish. Neotrop Ichthyol. Doi:10.1590/1982-0224-20170081.

Brodeur JC, Vera Candioti J, Damonte MJ, Bahl MF, Poliserpi MB, D’Andrea MF. 2020. Frog somatic indices: Importance of considering allometric scaling, relation with body condition and seasonal variation in the frog *Leptodactylus latrans*. Ecol Indic. Doi:10.1016/j.ecolind.2020.106496.

Burnham,KP, Anderson, DR. 2002. Model Selection and Multimodel Inference A Practical Information-Theoretic Approach. Second. Springer-Verlag, New York, 488 p.

Candolin U, Voigt HR. 2001. Correlation between male size and territory quality: Consequence of male competition or predation susceptibility? Oikos. Doi:10.1034/j.1600-0706.2001.950204.x.

Carey MP, Sanderson BL, Friesen TA, Barnas KA, Olden JD. 2011. Smallmouth bass in the pacific northwest: a threat to native species; a benefit for anglers. Rev. Fish. Sci. doi:10.1080/10641262.2011.598584.

Cargnelli LM, Gross MR. 1996. The temporal dimension in fish recruitment: Birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). Can J Fish Aquat Sci. doi:10.1139/f95-193.

Cargnelli LM, Gross MR. 1997. Notes: Fish energetics: larger individuals emerge from winter in better condition. Trans Am Fish Soc. Doi:10.1577/1548-8659(1997)126<0153:nfelie>2.3.co;2.

Chezik KA, Lester NP, Venturelli PA. 2014a. Fish growth and degree-days II: Selecting a base temperature for an among-population study. Can J Fish Aquat Sci. doi:10.1139/cjfas-2013-0615.

Chezik KA, Lester NP, Venturelli PA. 2014b. Fish growth and degree-days I: Selecting a base temperature for a within-population study. Can J Fish Aquat Sci. doi:10.1139/cjfas-2013-0295.

Ciuti S, Apollonio M. 2016. Reproductive timing in a lekking mammal: Male fallow deer getting ready for female estrus. Behav Ecol. Doi:10.1093/beheco/arw076.

Clarke A, Johnston NM. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol. Doi:10.1046/j.1365-2656.1999.00337.x.

Colchen T, Teletchea F, Fontaine P, Pasquet A. 2017. Temperature modifies activity, inter-individual relationships and group structure in a fish. Curr Zool. Doi:10.1093/cz/zow048.

Côte IM, Hunte W. 1989. Male and female mate choice in the redlip blenny: why bigger is better. Anim Behav. Doi:10.1016/S0003-3472(89)80067-3.

Cuadrado M, Loman J. 1999. The effects of age and size on reproductive timing in female *Chamaeleo chamaeleon*. J Herpetol. Doi:10.2307/1565536.

Danylchuk AJ, Fox MG. 1994. Age and size-dependent variation in the seasonal timing and probability of reproduction among mature female pumpkinseed, *Lepomis gibbosus*. Environ Biol Fishes. Doi:10.1007/BF00004929.

Descamps S, Bêty J, Love OP, Gilchrist HG. 2011. Individual optimization of reproduction in a long-lived migratory bird: A test of the condition-dependent model of laying date and clutch size. Funct Ecol. Doi:10.1111/j.1365-2435.2010.01824.x.

Dickerson BR, Brinck KW, Willson MF, Bentzen P, Quinn TP. 2005. Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. Ecology. Doi:10.1890/03-625.

Dickerson BR, Quinn TP, Willson MF. 2002. Body size, arrival date, and reproductive success of pink salmon, *Oncorhynchus gorbuscha*. Ethol Ecol Evol. Doi:10.1080/08927014.2002.9522759.

Dobson FS, Michener GR. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology. Doi:10.2307/1939350.

Dufresne F, Fitzgerald GJ, Lachance S. 1990. Age and size-related differences in reproductive success and reproductive costs in threespine sticklebacks (*Gasterosteus aculeatus*). Behav Ecol. Doi:10.1093/beheco/1.2.140.

Essington TE, Quinn TP, Ewert VE. 2000. Intra- and inter-specific competition and the reproductive success of sympatric Pacific salmon. Can J Fish Aquat Sci. doi:10.1139/f99-198.

Franckowiak RP, Ridgway MS, Wilson CC. 2017. Genetic mating system and mate selection in smallmouth bass. Ecol Evol. doi:10.1002/ece3.3423

Fullerton AH, Garvey JE, Wright RA, Stein RA. 2000. Overwinter growth and survival of largemouth bass: interactions among size, food, origin, and winter severity. Trans Am Fish Soc. Doi:10.1577/1548-8659(2000)129<0001:ogasol>2.0.co;2.

Gibbons DW. 1989. Seasonal reproductive success of the Moorhen *Gallinula chloropus*: the importance of male weight. Ibis (Lond 1859). Doi:10.1111/j.1474-919X.1989.tb02744.x.

Gillooly JF, Baylis JR. 1999. Reproductive success and the energetic cost of parental care in male smallmouth bass. J Fish Biol. Doi:10.1006/jfbi.1998.0888.

Hennin HL, Bêty J, Legagneux P, Gilchrist HG, Williams TD, Love OP. 2016. Energetic physiology mediates individual optimization of breeding phenology in a migratory arctic seabird. Am Nat. doi:10.1086/688044

Hewitt BA, Lopez LS, Gaibisels KM, Murdoch A, Higgins SN, Magnuson JJ, Paterson AM, Rusak JA, Yao H, Sharma S. 2018. Historical trends, drivers, and future projections of ice phenology in small north temperate lakes in the laurentian great lakes region. Water. Doi:10.3390/w10010070

Hinch SG, Collins NC. 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: Insights from direct video observations. Trans Am Fish Soc. Doi:10.1080/1548-8659(1991)120[0657:IODANN]2.3.CO;2.

Hovel RA, Carlson SM, Quinn TP. 2017. Climate change alters the reproductive phenology and investment of a lacustrine fish, the three-spine stickleback. Glob Chang Biol. Doi:10.1111/gcb.13531.

Hubbs CL, Bailey RM. 1938. The small-mouthed bass. Cranbrook Institute of Science Bulletin 10. 92 pp.

Hurst TP, Conover DO. 2003. Seasonal and interannual variation in the allometry of energy allocation in juvenile striped bass. Ecology. Doi:10.1890/02-0562.

Jørgensen CB. 1982. Factors controlling the ovarian cycle in a temperate zone anuran, the toad *Bufo bufo*: Food uptake, nutritional state, and gonadotropin. J Exp Zool. Doi:10.1002/jez.1402240317

Karino K. 1995. Male-male competition and female mate choice through courtship display in the territorial damselfish *Stegastes nigricans*. Ethology. Doi:10.1111/j.1439-0310.1995.tb00320.x.

Kaufman SD, Johnston TA, Leggett WC, Moles MD, Casselman JM, Schulte-Hostedde AI. 2007. Relationships between body condition indices and proximate composition in adult walleyes. Trans Am Fish Soc. Doi:10.1577/T06-262.1

Kim D, Taylor AT, Near TJ. 2022. Phylogenomics and species delimitation of the economically important Black Basses (Micropterus). Sci Rep. doi:10.1038/s41598-022-11743-2

Kleiber M. 1947. Body size and metabolic rate. Physiol Rev. doi:10.1152/physrev.1947.27.4.511.

Knapp RA, Vredenburg VT. 1996. Spawning by California golden trout: characteristics of spawning fish, seasonal and daily timing, redd characteristics, and microhabitat Preferences. Trans Am Fish Soc. Doi:10.1577/1548-8659(1996)125<0519:sbcgtc>2.3.co;2.

Lane JE, Boutin S, Gunn MR, Coltman DW. 2009. Sexually selected behaviour: Red squirrel males search for reproductive success. J Anim Ecol. Doi:10.1111/j.1365-2656.2008.01502.x.

Langston NE, Freeman S, Rohwer S, Gori D. 1990. The evolution of female body size in red-winged blackbirds: the effects of timing of breeding, social competition, and reproductive energetics. Evolution (N Y). doi:10.1111/j.1558-5646.1990.tb05247.x.

Lasiewski RC, Dawson WR. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor. Doi:10.2307/1366368.

Le Boeuf BJ. 1974. Male-male competition and reproductive success in elephant seals. Integr Comp Biol. Doi:10.1093/icb/14.1.163.

Long J, Allen M, Porak W, Suski C. 2015. A historical perspective of black bass management in the United States. Am Fish Soc Symp.

Lucifora LO, García VB, Menni RC, Escalante AH, Hozbor NM. 2009. Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. Eco Res. Doi:10.1007/s11284-008-0487-z.

Lukas JA, Orth DJ. 1995. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. Trans Am Fish Soc. Doi:10.1577/1548-8659(1995)124<0726:fansos>2.3.co;2.

Lyons J, Kanehl P. 2002. Seasonal movements of smallmouth bass in streams. Am Fish Soc Symp 31, 149-160.

Mackereth RW, Noakes DLG, Ridgway MS. 1999. Size-based variation in somatic energy reserves and parental expenditure by male smallmouth bass, *Micropterus dolomieu*. Env Biol Fish. Doi:10.1007/978-94-017-3678-7_19

[dataset] Magnuson, J., S. Carpenter, and E. Stanley. 2020. North Temperate Lakes LTER: High Frequency Meteorological and Dissolved Oxygen Data – Sparkling Lake Raft 1989 – current ver 32. Environmental Data Initiative. https://doi.org/10.6073/pasta/101ae920e5b5a97fadd3cb439440ac3f.

Makarieva AM, Gorshkov VG, Li B, Chown SL, Reich PB, Gavrilov VM. 2008. Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum. Proc Natl Acad Sci. https://doi.org/10.1073/pnas.0802148105

McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): Do larger, heavier males gain greater mating success? Behav Ecol Sociobiol. Doi:10.1007/s002650000293.

Munther GL. 1970. Movement and distribution of smallmouth bass in the Middle Snake River. Trans Am Fish Soc. Doi:10.1577/1548-8659(1970)99<44:madosb>2.0.co;2.

Neuheimer AB, Taggart CT. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Can J Fish Aquat Sci 64, 375-385.

Nagy KA. 2005. Field metabolic rate and body size. J Exp Biol. Doi:10.1242/jeb.01553.

Newbolt CH, Acker PK, Neuman TJ, Hoffman SI, Ditchkoff SS, Steury TD. 2017. Factors influencing reproductive success in male white-tailed deer. J Wildl Manage. Doi:10.1002/jwmg.21191.

Oliver JD, Holeton GF, Chua KE. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Trans Am Fish Soc. Doi:10.1577/1548-8659(1979)108<130:omofsb>2.0.co;2.

Ongarato RJ, Snucins EJ. 1993. Aggression of guarding male smallmouth bass (*Micropterus dolomieui*) towards potential brood predators near the nest. Can J Zool. Doi:10.1139/z93-062.

Piché J, Hutchings JA, Blanchard W. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. Proc B. doi:10.1098/rspb.2008.0251.

Post DM. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. Ecology. Doi:10.1890/0012-9658(2003)084[1298:IVITTO]2.0.CO;2.

Post DM, Kitchell JF, Hodgson JR. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. Can J Fish Aquat Sci. doi:10.1139/f98-139.

Post JR, Evans DO. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Can J Fish Aquat Sci. doi:10.1139/f89-246.

Raffetto NS, Baylis JR, Serns SL. 1990. Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus dolomieui*). Ecology. Doi:10.2307/1938289.

Ridgway MS. 1988. Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieui*). Can J Zool. Doi:10.1139/z88-248.

Ridgway MS, Shuter BJ, Post EE. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). J Anim Ecol. Doi:10.2307/5304.

Ridgway MS, Shuter BJ. 1994. The effects of supplemental food on reproduction in parental male smallmouth bass. Env Biol Fish. Doi:10.1007/BF00004938

Ridgway MS. 1989. The parental response to brood size manipulation in smallmouth bass (*Micropterus dolomieui*). Ethology. Doi:10.1111/j.1439-0310.1989.tb00728.x.

Ridgway MS, Friesen TG. 1992. Annual variation in parental care in smallmouth bass, *Micropterus dolomieu*. Environ Biol Fishes. Doi:10.1007/BF00001890.

Schloesser RW, Fabrizio MC. 2017. Condition indices as surrogates of energy density and lipid content in juveniles of three fish species. Trans Am Fish Soc. Doi:10.1080/00028487.2017.1324523

Saunders R, Bozek MA, Edwards CJ, Jennings MJ, Newman SP. 2002. Habitat features affecting smallmouth bass *Micropterus dolomieu* nesting success in four northern Wisconsin lakes. Am Fish Soc Symp 31, 123-134.

Schreer JF, Cooke SJ. 2002. Behavioral and physiological responses to smallmouth bass to a dynamic thermal environment. Am Fish Soc Symp 31, 191-203

Shuter BJ, Finstad AG, Helland IP, Zweimüller I, Hölker F. 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquat Sci. doi:10.1007/s00027-012-0274-3.

Shuter BJ, Maclean JA, Fry FEJ, Regier HA. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans Am Fish Soc. Doi:10.1577/1548-8659(1980)109<1:ssoteo>2.0.co;2.

Shuter BJ, Post JR. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans Am Fish Soc. Doi:10.1577/1548-8659(1990)119<0314:cpvatz>2.3.co;2.

Shuter BJ, Ridgway MS. 2002. Bass in time and space: operational definitions of risk. Am Fish Soc Symp 31, 235-249.

Sih A, Lauer M, Krupa JJ. 2002. Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water striders. Anim Behav. Doi:10.1006/anbe.2002.2002.

Smallegange IM. 2010. Complex environmental effects on the expression of alternative reproductive phenotypes in bulb mite. Evo Eco. Doi:10.1007/s10682-010-9446-6.

Stiver KA, Alonzo SH. 2010. Large males have a mating advantage in a species of darter with smaller, allopaternal males *Etheostoma olmstedi*. Curr Zool. Doi:10.1093/czoolo/56.1.1.

Suski CD, Ridgway MS. 2007. Climate and body size influence nest survival in a fish with parental care. J Anim Ecol. Doi:10.1111/j.1365-2656.2007.01242.x

Tejedo M. 1992. Effects of body size and timing of reproduction on reproductive success in female natterjack toads (*Bufo calamita*). J Zool. Doi:10.1111/j.1469-7998.1992.tb04454.x.

Thomas SC, Ickes K. 1995. Ontogenetic Changes in Leaf Size in Malaysian Raid Forest Trees. Biotrop. Doi:10.2307/2388954.

Todd BD, Scott DE, Pechmann JHK, Whitfield Gibbons J. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. Proc R Soc B Biol Sci. doi:10.1098/rspb.2010.1768.

Visser ME, Both C. 2005. Shifts in phenology due to global climate change: The need for a yardstick. Proc R Soc B Biol Sci. doi:10.1098/rspb.2005.3356.

Welsh DP, Wiegmann DD, Angeloni LM, Newman SP, Miner JG, Baylis JR. 2017. Condition-dependent reproductive tactics in male smallmouth bass: evidence of an inconsistent birthdate effect on early growth and age at first reproduction. J Zool. Doi:10.1111/jzo.12454.

West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling laws in biology. Science (80-). Doi:10.1126/science.276.5309.122.

Wiegmann DD, Baylis JR, Hoff MH. 1992. Sexual selection and fitness variation in a population of smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). Evolution (N Y). doi:10.1111/j.1558-5646.1992.tb01166.x.

Wiegmann DD, Baylis JR. 1995. Male body size and paternal behaviour in smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). Anim Behav. Doi:10.1016/0003-3472(95)80010-7.

Wiegmann DD, Baylis JR, Hoff MH. 1997. Male fitness, body size and timing of reproduction in smallmouth bass, *Micropterus dolomieui*. Ecology. Doi:10.2307/2265983.

Wilmes JC, Hoey AS, Pratchett MS. 2020. Contrasting size and fate of juvenile crown-of-thorns starfish linked to ontogenetic diet shifts. Proc B. doi:10.1098/rspb.2020.1052.

Wong BBM, Candolin U. 2005. How is female mate choice affected by male competition? Biol Rev Camb Philos Soc. Doi:10.1017/S1464793105006809.

Yasuno N, Chiba Y, Shindo K, Fujimoto Y, Shimada T, Shikano S, Kikuchi E. 2012. Size-dependent ontogenetic diet shifts to piscivory documented from stable isotope analyses in an introduced population of largemouth bass. Env Bio Fish. Doi:10.1007/s10641-011-9911-2.

FIGURE LEGENDS

Figure 1. Relationship between the degree days accumulated before the first average daily water temperature of 15 ºC (dashed line) and the reproductive response time–the days between the date on which the mean water temperature first reached 15 ºC and the median date on which eggs were found in nests–of the population each year.

Figure 2. Relationships between parental male length (ln transformed) and the degree days accumulated before eggs were observed in nests (ln transformed) for 1999, 2001-2009. The trend line depicts the projected relationship for males with mean condition while the light blue shading depicts relationships for males from 1st percentile to 99th percentile condition. These far extremes of condition were selected so that the impact of condition could be better visualized, as it was minimal. Data are presented on ln-scaled axes and jittered along the y-axis to reveal overlapping points.

TABLES AND TABLE LEGENDS

Table 1

Male smallmouth bass and temperature characteristics across the 10-year dataset.

Year	Males on Nests	Males with Eggs	Average Size of Males with Eggs (cm)	Winter Length (days)	Mean Temp (ºC)	DD before 15 ºC	Size Threshold
1999	102	88	32.0 ± 0.7	—	19.3	57.4	42,2
2001	152	101	30.3 ± 0.7	174	18.9	35.6	41.4
2002	221	147	30.9 ± 0.5	211	20.1	14.8	40.0
2003	234	149	32.5 ± 0.5	192	18.7	47.0	41.6
2004	284	159	32.4 ± 0.6	190	17.4	67.2	42.7
2005	216	110	32.3 ± 0.6	186	19.7	20.8	41.7
2006	188	147	34.3 ± 0.4	186	19.8	27.9	41.3
2007	157	107	34.9 ± 0.5	198	18.7	16.4	42.0
2008	198	139	35.4 ± 0.5	192	18.4	32.1	44.1
2009	176	114	34.0 ± 0.5	180	17.8	36.25	41.4

Temperature data for 1998 were not collected and, hence, winter length before the 1999 reproductive season was not computed. Degree days (DD) were calculated using the threshold T_0 = 10 °C. Temperature and Maximum are abbreviated as Temp and Max.

FIGURES

Figure 1.

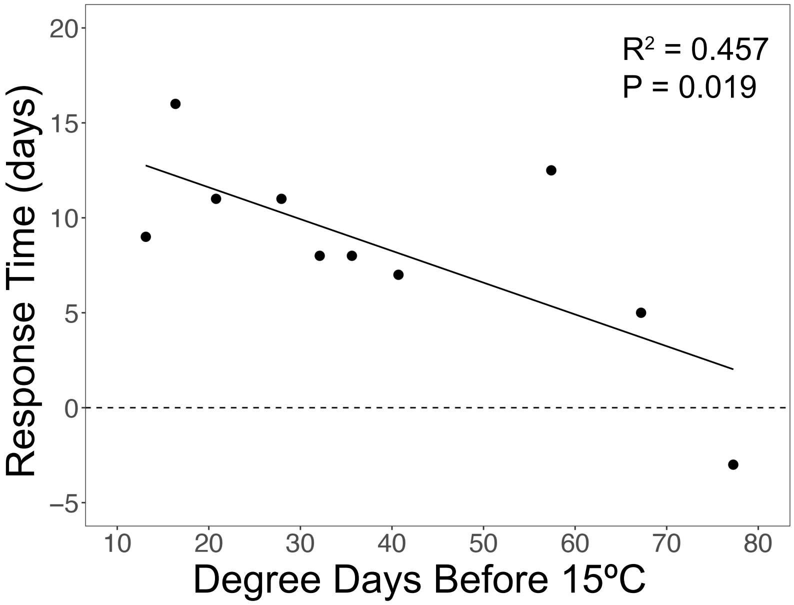
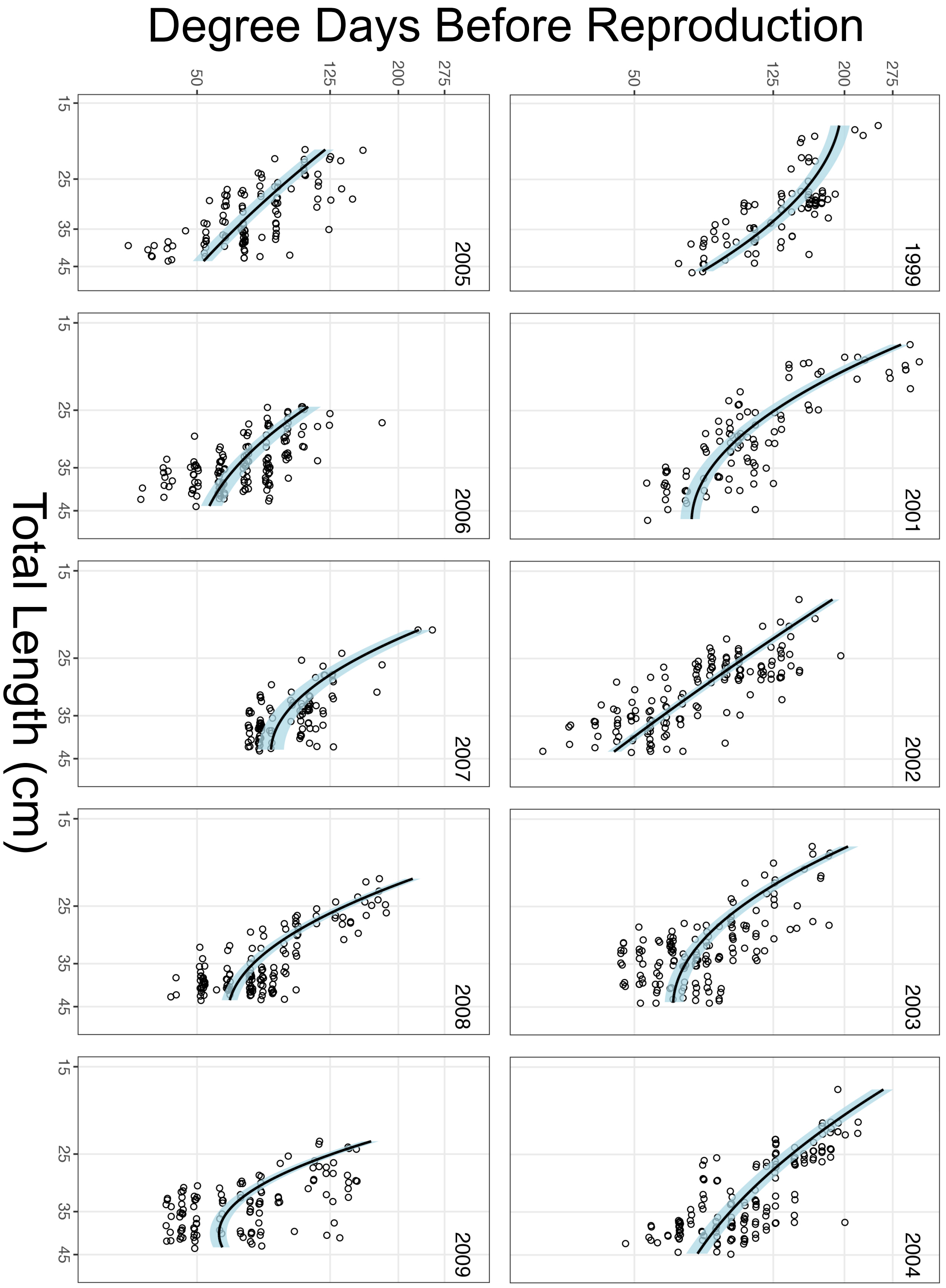


Figure 2.


Degree Days Before Reproduction
Total Length (cm)
50
125
200
275
15
25
35
45
2005
2006
2007
2008
2009
1999
2001
2002
2003
2004