Is energetics or competition a stronger driver of male smallmouth bass seasonal reproductive timing?

Running title: Energetics or Competition?

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LAY SUMMARY

In many animals, larger individuals reproduce earlier in a season. We collected data on reproductive timing in a wild population of bass, and examined whether bigger males breed earlier because they are better competitors, or because they are energetically prepared to breed earlier in the season. Our results suggest that larger males reproduce earlier in a season because they recuperate energy lost in the over-winter period of starvation more rapidly, not because of competitive advantage.

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ABSTRACT

Intraspecific competitive ability is often associated with body size and has been shown to influence reproductive timing in many species. However, energetic constraints provide an alternative explanation for size-related differences of reproductive timing. In temperate fishes that experience a winter starvation period, for instance, a negative allometric relationship between body size and winter energy loss might explain why larger males spawn earlier in a season than smaller males, especially in fishes that exhibit paternal care, which is energetically costly and limits parental foraging opportunities. Male smallmouth bass, *Micropterus dolomieu*, defend nesting territories in which they care for offspring over an extended period. In northern populations, males rely on energy reserves over a winter starvation period and in spring must recoup energy losses before initiating reproduction, making them ideal systems in which to study contributions of competition and energetic allometry on differences of reproductive timing. Here, we harness data on parental male *M. dolomieu* from a 10-year study and show that larger males required fewer degree days—a measure of thermal energy experienced—in spring before they spawned each year and that the time of peak seasonal reproduction in the population was negatively related to the number of degree days accumulated before reproduction started. Furthermore, we found that growth of individual males between seasons better predicted changes in timing of reproduction

than changes in size relative to competitors. Together, these results suggest that timing of reproduction in this population is more strongly influenced by energetic constraints than size-based competition amongst males.

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

INTRODUCTION

Intraspecific competition has a strong influence on reproductive success in many species (Boeuf 1974; Essington et al. 2000; Wong and Candolin 2005; Boesch et al. 2006; Lane et al. 2009). When competition is between males, body size is often the factor that determines which individuals have a competitive advantage (Alcock 1994; Candolin and Volgt 2001; McElligott et al. 2001; Sih et al. 2002; Newbolt et al. 2016). It comes as no surprise, then, that many studies have found evidence that larger males outcompete smaller males for mates and breed earlier than smaller males, both within and between reproductive seasons (Côte and Hunte 1989; Gibbons 1989; Dufresne et al. 1990; Dickerson et al. 2002; Ciuti and Apollonio 2016).

However, there is an alternative explanation for why bigger individuals of some species breed earlier. In diverse taxa, including fishes, reptiles, insects, amphibians, birds and mammals, larger individuals use less energy proportionate to their mass than smaller individuals (i.e., they show negative allometric relationships with 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; Brodeur et al. 2020). These relationships imply that smaller males will require more time to accumulate energy stores prior to reproduction in species that, say, experience a winter dormant period. Indeed, energetic constraints are known to produce a negative relationship between body size and reproductive timing in a number of species (Tejedo 1992; Danylchuk and Fox 1994; Dobson and Michener 1995; Descamps et al. 2011).

In fishes, where indeterminate growth can lead to substantial variation in size among mature adults, there is an increased opportunity for size to play a role in reproductive timing (Ridgway and Friesen 1992; Knapp et al. 1996; Wiegmann et al. 1997; Dickerson et al. 2005). 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). Indeed, when males compete for a breeding territory or mates, larger males often have a distinct advantage (Karino 1995; Candolin and Volgt 2001; Stiver and Alonzo 2010). However, a negative allometric relationship to mass specific basal metabolism has also been noted in fishes (Shuter and Post 1990; Cargnelli and Gross 1997; Clarke and Johnston 1999). In north-temperate fishes, where males rely entirely on stored energy reserves throughout winter, such a negative allometric relationship could explain why larger males, which lose proportionately less of their winter energy reserves, spawn earlier in a season than smaller males (Post and Evans 1989; Ridgway et al. 1991; Fullerton et al. 2000). In fishes that exhibit male territoriality and paternal care, both energetics and competitive interactions may contribute to variation in reproductive timing, as is known to occur in other taxa (Langston et al. 1990; Cuadrado and Loman 1999).

Here, we use a 10-year dataset on smallmouth bass, *Micropterus dolomieu*, to tease apart the influence of competition and energetics on reproductive timing. In particular, we follow the reproductive behavior of individual males throughout their lives in a closed population to investigate how male body size, thermal history, and competitive ability impact reproductive timing. There is some evidence that energetics, rather than competition, constrains reproductive timing in *M. dolomieu* (Ridgway et al. 1991; Gillooly

87 and Baylis 1999). However, other aspects of their biology, such as a female preference
88 for larger males and aggressive male-to-male territorial interactions, could also impact
89 reproductive timing (see Ridgway 1988; Ridgway 1989; Baylis et al. 1993; Ongarato and
90 Snucins 1993; Wiegmann et al. 1992; Wiegmann and Baylis 1995). First, we test the
91 hypothesis that larger males reproduce earlier in the spring after the accumulation of
92 fewer degree days, a measure of the thermal energy experienced by an individual. Then,
93 we consider the reproductive timing of the population and test the hypothesis that timing
94 of peak reproduction is negatively related to the number of degree days accumulated
95 before reproduction starts in the spring. Finally, we use comparisons of change in
96 individual male length versus change in competitive status across years to test the
97 hypothesis that an energetic rather than competitive advantage of large body size better
98 predicts changes in within-season reproductive timing.
99

100 **MATERIALS AND METHODS**

101 Natural history

102 Smallmouth bass, *Micropterus dolomieu*, are native to North America and reproduce
103 seasonally, when water temperatures approach 15 ºC (Hubbs and Bailey 1938; Shuter
104 et al. 1980). Males construct nests in the littoral zone into which females deposit eggs.
105 Typically, males mate with only one female and researchers have observed no sneaker
106 behavior (Ridgway 1989; Raffetto et al. 1990; Wiegmann et al. 1992). After spawning,
107 males remain in close proximity to their nest and defend offspring until their fry swim up
108 and disperse, a period that may last several weeks (Hinch and Collins 1991). Parental
109 behavior is costly and leads to a net loss of lean mass, as males rarely feed in this
110 period (Gillooly and Baylis 1999). The energetic cost of parental care in combination with

the fact that smaller males end winter with a proportionately larger energy deficit than larger males may allow larger males to spawn earlier within a season than smaller males (Ridgway et al. 1991). In northern populations, smallmouth bass activity ceases when temperatures drop below 10 ºC and individuals are largely dormant over winter (Hubbs and Bailey 1938; Munther 1970; Oliver et al. 1979; but see Lyons and Kanehl 2002; Schreer and Cooke 2002).

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. Saunders et al. (2002) describe the benthic and limnological characteristics of the lake in detail. Anglers are subject to a mandatory creel census. 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. From 1999-2006 only 7% of breeding males were larger than 41 cm and from 2007 onward no breeding males were larger than the 51 cm size limit (Table 1).

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 found in studies of other Wisconsin lakes (Bozek et al. 2002). Snorkelers placed a numbered tag constructed from a strip of Rite-n-Rain paper tied to a sinker on the edge of each nest and recorded the date, stage of embryos (if present), depth, location and distinctive landmarks that might be useful to relocate a nest when each nest was discovered. They also recorded the developmental stage of any progeny at each subsequent visit to nests, where progressive ontogenetic stages were categorized as eggs, clear fry, grey fry, black-striped fry, black fry or swim-up fry.

Characteristics of parental males

We captured parental males from their nests with hand nets and recorded their total length (cm). We used uniquely numbered Floy FD-67C anchor tags to track males across years (University of Wisconsin RARC protocol A-48-9700-L00173-2-04-99). We estimated competitors as the number of unique nesting males captured each season (Table 1). We also calculated the average size of these competitors each year. Further, we calculated average growth (cm) and change in competitive ability (i.e., body size, ranked relative to other parental males in a season) for males who bred in consecutive years (Table 1).

Temperature and degree days

We used temperature data to estimate the thermal energy experienced by parental males prior to reproduction 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 an unknown person) resulted in some missing temperature records. We estimated these records using regression equations that characterized the relationship between water temperature in 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 (Supplement; Supplementary Figure S1; Supplementary Table S1).

Each year we define the growth season as the period between the first day the average temperature climbed above 10 ºC and the last day before average temperature dropped below 10 ºC (Shuter et al., 1980; Ridgway et al., 1991). We calculated the average and maximum temperature of the growth season for every year. We also calculated winter length, defined as the number of days between growth seasons (Table 1).

We calculated degree days, a measure of the thermal energy experienced by an individual, as the sum of positive differences between the average daily water temperature at 1 m and the threshold T_0 = 10 °C for each day up to some specified time period (Shuter et al. 1980; Ridgway et al. 1991; Lukas and Orth 1995; Welsh et al. 2017; reviewed by Chezik et al. 2014a, b). In particular, we summed degree days each year from the first date on which the water temperature exceeded 10 °C until the date at which eggs were found in the nest of a male to produce a measure of the seasonal thermal energy experienced by each parental male prior to reproduction (Shuter et al. 1980; Ridgway et al. 1991). In addition, for each year we calculated the number of

183 degree days accumulated by the date that the average water temperature reached 15
184 ºC, the temperature at which reproductive activity is typically initiated. We used this to
185 predict a population-level response time to the rate at which the water temperature
186 increased, where the response time is the interval (days) between the date on which the
187 mean water temperature first reached 15 ºC and the median date on which eggs were
188 found in nests (Shuter et al. 1980).
189

190 Statistical analyses

191 *Individual behavioral response to temperature*

192 We used linear mixed models to determine the relationship between male total length
193 ($\log_e$ transformed) and the number of degree days ($\log_e$ transformed, threshold T_0 = 10
194 °C) that had accumulated up to the date on which a male spawned (i.e., the date a nest
195 was found to contain eggs), where individual was included as a random effect (because
196 316 individuals bred in more than one season). We fit models with and without year as a
197 covariate and with and without an interaction term between year and male total length
198 and the Akaike information criterion was used to choose between models (Akaike 1973).
199 We restricted the analysis to the first date that a male spawned within a year, if a male
200 spawned more than once within a season (N = 127). We excluded males on nests that
201 were discovered after eggs had hatched from the analysis. The total sample included
202 1,261 observations. If larger males experience less severe winter energy losses, then
203 the slope of the coefficient associated with male length is expected to be negative in
204 each year (Ridgway et al. 1991).
205

206 *Population-level responses to temperature*

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 temperature controls individual reproductive readiness, then we expect the slope of this relationship to be negative (Shuter et al. 1980).

Energetics versus competition

We used a subset of males (N = 265) that spawned in consecutive years to disentangle the potential influences of competition and thermal history on within-season reproductive timing. If the negative allometric association between male body size and winter energy losses controls reproductive timing, then a large increase in male length in a particular year should result in a large decrease in the degree days accumulated before reproduction in the subsequent year. If reproductive timing is controlled by male competitive ability, in contrast, then a male should spawn earlier in a season when confronted with competitors that are relatively small and shifts in competitive status should explain differences of reproductive timing between years. We ranked all males that spawned in each year based on their total lengths, assigning the largest male a rank of zero and smaller males consecutively larger integers (same-sized males received mid-ranks). Notably, this means that a decrease in rank by a male that spawned in two consecutive years corresponds to an increase in size relative to competitors. We used the change of male rank for males that spawned in consecutive years to predict the difference in accumulated degree days before reproduction between years.

We created linear models using either change in rank or change in length ($\log_e$ transformed) between consecutive years to determine the extent to which either factor predicted the respective yearly change in degree days ($\log_e$ transformed) accumulated before individuals reproduced. We also computed the correlation between change in rank and change in length for each year to determine the strength of the association between the two factors (Table 2). Due to the fact that some males appeared in more years than others, it was not possible to include all years in a single analysis with a random effect for individual. Consequentially, we created separate models for each pair of consecutive years to ensure independence of statistics. These models were then compared using the Akaike information criterion (Table 2).

RESULTS

Characteristics of parental males and seasonal temperature variation

Males were caught over 2,055 nests throughout the course of the study and 847 unique males were tagged. We failed to catch 5.39% of parental males from nests throughout the course of the study. The most males we ever failed to catch in a year was 26 (in 2005). 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 ranged from 102 to 284. The total length of males in our data set ranged from 17 cm to 47.5 cm (N = 1261) and the seasonal average ranged from 29.8 to 35.1 cm. The mean change in rank and change in size between males that reproduced in consecutive years ranged from –20.0 to –59 (a negative change in rank indicates an increase in relative size) and 2.5 to 5.4 respectively (Table 1). Temperature patterns also varied year by year. Winter length ranged from 174 days before the 2001 reproductive season to 211 days before the 2002

255 reproductive season. The mean and maximum temperatures of the growth season
256 ranged from 17.4 to 20.1 ºC and 23.7 to 27.2 ºC, respectively (Table 1).
257

258 Responses to temperature

259 *Individual behavior*

260 In all ten years of the study, a linear relation with negative slope linked male total length
261 ($\log_e$ transformed) to the degree days a male accumulated prior to reproduction (Figure
262 1). The model that was best supported by the Akaike information criterion had a weight
263 of 0.98, included year and male total length, and no interaction term between these two
264 factors (N = 1261, R^2 = 0.63, P < 0.0001; Figure 1). The common coefficient for male
265 total length was b = -1.27 ± 0.035. The year effect indicates that the y-intercepts differed
266 significantly between seasons (Figure 1).
267

268 *Population-level responses*

269 The dates on which peak reproduction occurred ranged from 23 May in 2001 to 10 June
270 10 in 2004. The degree days accumulated before the first day that temperatures reached
271 an average of 15 ºC varied greatly between years, from 13.1 in 2002 to 77.3 in 2009. In
272 years where more degree days accumulated before the first 15 ºC day, the population-
273 level response time was shorter (N = 9, r^2 = 0.46, P = 0.02; Figure 2). Indeed, in 2009
274 peak reproduction actually occurred 3 days before the first day that the average
275 temperature reached 15 ºC.
276

277 Energetics versus competition

In 1,009 instances, a male was captured from a nest in consecutive years and for a subset of 444 of these cases—265 unique individuals—the date on which a male spawned (i.e., its nest was discovered with eggs) was known in both years. The difference in male total length between the two years was a significant predictor of the difference in the number of degree days before reproduction in five out of eight (62.5%) of consecutive year pairs, where males that grew more showed larger reductions in degree days before they spawned between the two years (R^2 = 0.08-0.47; Figure 3; Table 2). In comparison, the difference in male rank relative to competitors between the two years was a significant predictor of the change of timing in just three out of the eight (37.5%) of year pairs, where a reduction of body size rank (i.e., increase of competitive status) was associated larger reductions in degree days before they spawned between the two years (R^2 = 0.08-0.29; Table 2). In every year where the relationship between either difference in length or difference in rank was a significant predictor of the difference in the number of degree days before reproduction , models that used difference in length as a predictor received greater weights using the Akaike information criterion (Table 2).

Notably, the change of male length between years was a significant predictor in all three year pairs in which the change of male competitive status was a significant predictor. Indeed, in all year pairs—even the two year pairs for which the change in male total length alone predicted the seasonal change of reproductive timing—the two predictors were highly correlated (Table 2). Furthermore, male competitive status appears to have been influential only when the change of male length between years had the strongest associations with changes of reproductive timing ($R^2 > 0.2$). Together, these results

302 suggest that the ostensible contribution of competitive status on reproductive timing was
303 an artifact of its correlation with male growth between years.
304

305 DISCUSSION

306 The observed patterns of reproductive timing at both the individual and population level
307 suggest that energetics, rather than competition, explains why larger male *M. dolomieu*
308 spawn earlier in a season than smaller males. Larger males spawned after an
309 accumulation of fewer degree days post winter dormancy than smaller males in all 10
310 years of the study. At the population level, the delay between the temperature cue that
311 triggers reproduction and the date of peak reproduction was shorter in years where more
312 degree days accumulated prior to the temperature signal. Higher thermal energy
313 experienced by the population appears to drive the distribution of reproduction dates
314 closer to the environmental signal, presumably because males are able to recoup winter
315 energy losses and reach some threshold energetic reserve that is sufficient to carry
316 them through the parental period.
317

318 Energetics over competition

319 The observed changes of reproductive timing by males that spawned in two consecutive
320 years was better explained by their growth than by changes of their competitive status
321 relative to other males. The change of male total length between years predicted
322 changes of reproductive timing in five of the eight consecutive year pairs we examined,
323 whereas changes of male competitive status—the size-based rank of a male relative to
324 competitors—was a significant predictor of changes in reproductive timing in only three
325 year pairs (Table 2). In the three years where both change in length and change in size-

326 based rank were significant predictors, models using change in length received greater
327 weights based on the Akaike information criterion.
328
329 We could identify no social or environmental explanation for why a change in competitive
330 status would be important in some years rather than others (Table 1). The years 2002-
331 2003, 2006-2007 and 2008–2009, where changes of male competitive status appeared
332 to be influential, did not have a larger shift in the number of male competitors than other
333 year pairs, nor did males experience a greater change in status. Especially short winters
334 might in principle relax energetic constraints on reproductive timing and thereby enhance
335 the importance of competition, but none of these year pairs were separated by unusually
336 short winters. Long periods of high temperatures early in the season might have a
337 similar effect and, indeed, 2009 had the highest number of degree days (77.3)
338 accumulated before the average water temperature reached 15 ºC. However, this
339 explanation, too, seems unlikely, as 2007 had the second lowest number of degree days
340 (16.4) accumulated before the water temperature reached 15 ºC. Lastly, neither the
341 mean nor maximum water temperature, which are known to increase aggressive
342 behavior in fishes, were particularly high in these year pairs (Biro et al. 2010; Colchen et
343 al. 2017; Brandão et al. 2018; Angiulli et al. 2020; Table 1).
344
345 The size-based measure of competitive status (i.e., size rank relative to other males) we
346 used presumably also ranks males with regard to female preferences. Hence, female
347 mate preference probably contribute little influence on reproductive timing by males. The
348 female preference for larger males implied in earlier studies by positive correlations
349 between male body size and the number of eggs they acquired seems more likely

attributable to a size-related energetic constraint on reproductive timing in females that is similar to that of males (Ridgway et al. 1991; Wiegmann et al. 1992; Baylis et al. 1993).

The effect of growth on changes in reproductive timing was also not observed in all year pairs, but there is a seemingly straightforward explanation, namely that male growth varied considerably between years (Table 1; Figure 3). In year pairs for which no relationship was observed, there were few males that grew especially well and the range of growth was also small, both of which likely impeded the detection of an association (Figure 3). Indeed, the average range of growth in years in which growth was not a significant predictor of changes of reproductive timing was 6.03 cm, compared to 7.38 cm in years where growth was a significant predictor (Table 1).

Comparisons to previous studies

The control of reproductive timing by individual thermal history is in accord with an earlier study in which parental male removal was not followed by earlier occupancy of nests by smaller males, which would be expected if competition forced smaller males to breed later in the season (Ridgway et al. 1991). There is an additional similarity between our results and those of earlier studies that further supports our hypothesis that reproductive timing in *M. dolomieu* is driven by an underlying metabolic process. Both 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, respectively. In these studies, male length was regressed on degree days (both log 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) included data collected over six years and their analyses indicated that the slope of the relationship did not differ significantly across years. Here, we regressed degree days on male size because we wanted to know how body size influences the number of degree days accumulated by a male before he spawns. But, an equivalent regression analysis with our data (not shown) produced a slope of -0.375, which is remarkably similar to those found in these two earlier studies.

Neuheimer and Taggart (2007) found that a single parameterization of length-at-age as a function of degree days is sufficient to explain growth variation of fish that experience constant or variable water temperatures. The similarity of slopes that characterize the relationship between male body size and accumulated degree days prior to reproduction in geographically separated 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 explain reproductive timing in diverse systems. Indeed, Shuter and Ridgway (2002) were able to accurately predict *M. dolomieu* start and end reproduction dates based on the regression analysis of Ridgway et al. (1991) in ten water bodies that varied considerably with regard to water temperature and the size distribution of adult males. If competition were the underlying cause of differences in timing of reproduction by males of different sizes, then we would expect the slope to vary both between populations and within populations between years with differences of population density and physical attributes of adult males. The consistent nature of the relationship between male size and degree days before reproduction across the long duration of our study, which encompassed

398 considerable annual variability, provides added confidence that the similarity of slopes
399 between Ridgway et al. (1991) and Lukas and Orth (1995) was not coincidental.
400

401 Applications for management and conservation

402 For popular game fishes like smallmouth bass, which have a history of management that
403 stretches back nearly 200 years, the identification of broadly consistent behavior
404 between habitats may support current efforts focused on the restoration of native
405 populations (Long et al. 2015). In other high latitude North American fishes, especially
406 those that experience cold winters that impose energetic requirements for individual
407 survival, similar relationships between temperature, size and reproductive timing also
408 likely apply (e.g., Cargnelli and Gross 1997; Hurst and Conover 2003). Changing climate
409 conditions have the potential to greatly disrupt the dynamics of reproductive timing and
410 northern freshwater fish communities are particularly vulnerable to these changes
411 (Visser and Both 2005; Todd et al. 2011; Shuter et al. 2012; Hovel et al. 2017). For
412 example, shorter, less severe winters could relax energetic constraints and permit
413 smaller individuals to reproduce earlier in a season or even at an earlier age, with ample
414 energy reserves, and induce a reversal of control of reproductive timing from one based
415 on energetics to one more dependent on male competitive status. Because the transfer
416 of thermal heat from the environment to fishes accumulates with time, even small
417 changes of temperature over development might cause significant differences in growth
418 trajectories throughout the life of an individual (Neuheimer and Taggart 2007). Further
419 studies that address how energetic constraints and competition influence phenology will
420 be critical to understanding how population dynamics will change as temperatures
421 continue to shift across the globe.

422

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DATA AVAILABILITY STATEMENT

Data will be deposited in Dryad in accordance with the journal's data archiving guidelines upon acceptance of this manuscript.

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637

638 **FIGURE LEGENDS**

639

640 **Figure 1.** Relationships between parental male length ($\log_e$ transformed) and the degree
641 days accumulated before eggs were observed in nests ($\log_e$ transformed) for 1999,
642 2001-2009. Data are presented on log-scaled axes.

643

644 **Figure 2.** Relationship between the degree days accumulated before the first average
645 daily water temperature of 15 ºC (dashed line) and the reproductive response time of the
646 population each year.

647

648 **Figure 3.** Relationships between change in $\log_e$-transformed total length and change in
649 $\log_e$-transformed degree days before reproduction for males that spawned in
650 consecutive years. Trend lines are included in years where the relationship is significant.
651 The letter R is written under year pairs for which the change of rank was a significant
652 predictor. Data are summarized in Table 2.

653

654 # TABLES AND TABLE LEGENDS

655

656 **Table 1**

657 **Male smallmouth bass and temperature characteristics within and between years.**

Year	Males on Nests	Average Size (cm)	Rank Change	Size Change (cm)	Range of Growth	Winter Length (days)	Mean Temp (ºC)	Max Temp (ºC)	DD before 15 ºC
1999	102	31.4 ± 0.7	NA	NA	NA	NA	19.3	26.7	57.4
2001	152	29.9 ± 0.6	NA	NA	NA	174	18.9	24.8	35.6
2002	221	29.8 ± 0.4	-23.3 ± 1.8	5.2 ± 0.2	7.5	211	20.1	26.0	13.1
2003	234	32.3 ± 0.4	-23.6 ± 1.7	5.4 ± 0.2	8.3	199	18.7	24.5	40.7
2004	284	31.6 ± 0.4	-32.7 ± 1.4	4.0 ± 0.1	7.0	197	17.4	23.8	67.2
2005	216	31.9 ± 0.4	-59 ± 2.1	2.6 ± 0.1	4.7	186	19.7	27.2	20.8
2006	188	33.9 ± 0.4	-43.1 ± 1.8	4.8 ± 0.2	8.3	186	19.8	25.5	27.9
2007	157	35.1 ± 0.4	-39.2 ± 1.6	3.7 ± 0.2	6.4	198	18.7	25.9	16.4
2008	198	33.7 ± 0.4	-20.0 ± 1.3	3.0 ± 0.2	6.4	192	18.4	23.7	32.1
2009	176	34.8 ± 0.4	-23.4 ± 1.4	2.5 ± 0.2	6.4	181	17.8	23.9	77.3

658 Rank change and size (total length) change indicate mean differences ± SE from the previous
659 year. Range of growth indicates the difference between the largest and smallest change in length
660 of an individual from the previous year. Data were not collected in 1998 or 2000 and, hence,
661 these differences were not computed for 1999 or 2001. Degree days (DD) were calculated using
662 the threshold T_0 = 10 °C. Temperature and Maximum are abbreviated as Temp and Max.

663

664 **Table 2**

665 **Linear relationships between change in $\log_e$-transformed male length (ΔL) and**

666 **competitive status (ΔR) and the change in $\log_e$-transformed degree days (ΔDD) for**

667 **males breeding in consecutive years.**

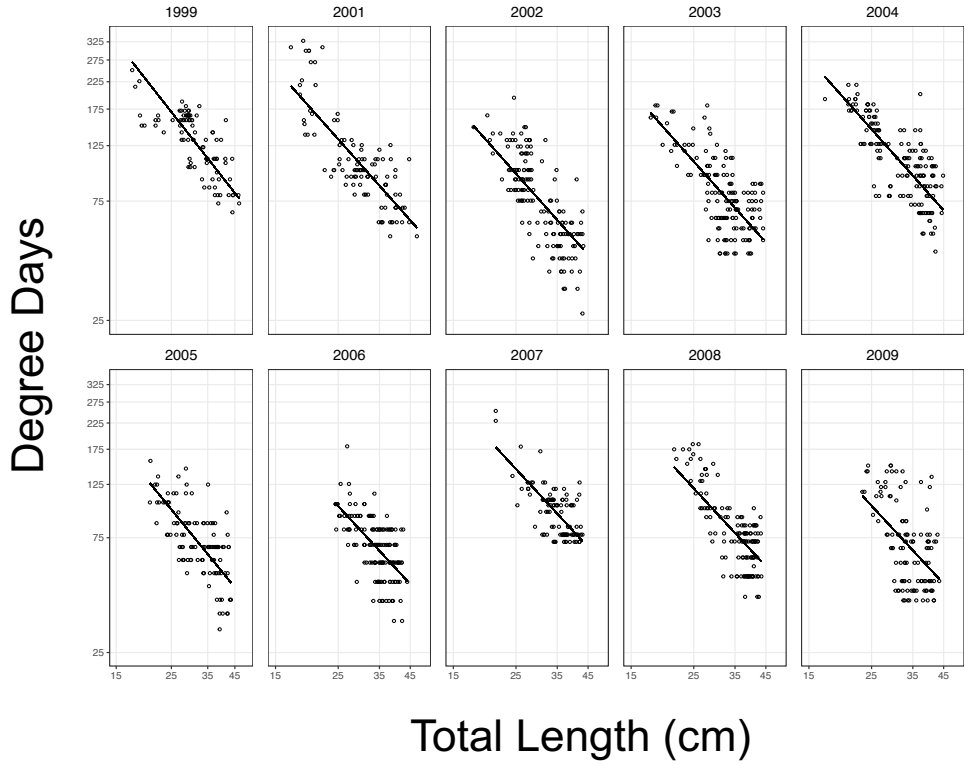
Year pair	*N*		Intercept	Coefficient	*Adjusted* R^2	*P*	AIC Weight	Correlation (Δ R, Δ L)
2001-2002	46	Δ R	-0.443	0.004	-0.008	0.420	0.09	*r* = -0.591
		Δ L	-0.271	-1.628	0.090	**0.024**	0.91	*P* < 0.001
2002-2003	61	Δ R	0.277	0.013	0.285	**< 0.001**	0.00	*r* = -0.821
		Δ L	0.611	-3.680	0.465	**< 0.001**	1.00	*P* < 0.001
2003-2004	60	Δ R	-0.018	-0.004	0.023	0.130	0.77	*r* = -0.867
		Δ L	0.104	0.103	-0.017	0.882	0.23	*P* < 0.001
2004-2005	44	Δ R	-0.401	0.003	0.027	0.148	0.37	*r* = -0.929
		Δ L	-0.424	-1.482	0.050	0.078	0.63	*P* < 0.001
2005-2006	49	Δ R	-0.101	0.003	0.051	0.064	0.34	*r* = -0.907
		Δ L	-0.103	-0.871	0.077	**0.030**	0.66	*P* < 0.001
2006-2007	62	Δ R	0.591	0.009	0.181	**< 0.001**	0.10	*r* = -0.862
		Δ L	0.548	-2.779	0.238	**< 0.001**	0.90	*P* < 0.001
2007-2008	65	Δ R	-0.301	0.0002	-0.016	0.931	0.50	*r* = -0.885
		Δ L	-0.309	0.052	-0.016	0.909	0.50	*P* < 0.001
2008-2009	57	Δ R	-0.063	0.009	0.084	**0.016**	0.02	*r* = -0.891
		Δ L	-0.019	-3.398	0.204	**< 0.001**	0.98	*P* < 0.001

668 Degree days were measured up until the point eggs were found in the nest of a male. Bold *P*

669 values indicate *P* < 0.05. The Akaike information criterion is abbreviated as AIC.

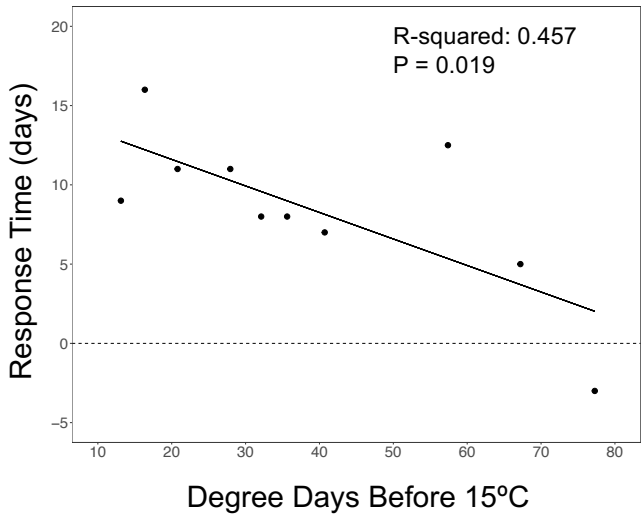
670

671 **FIGURES**



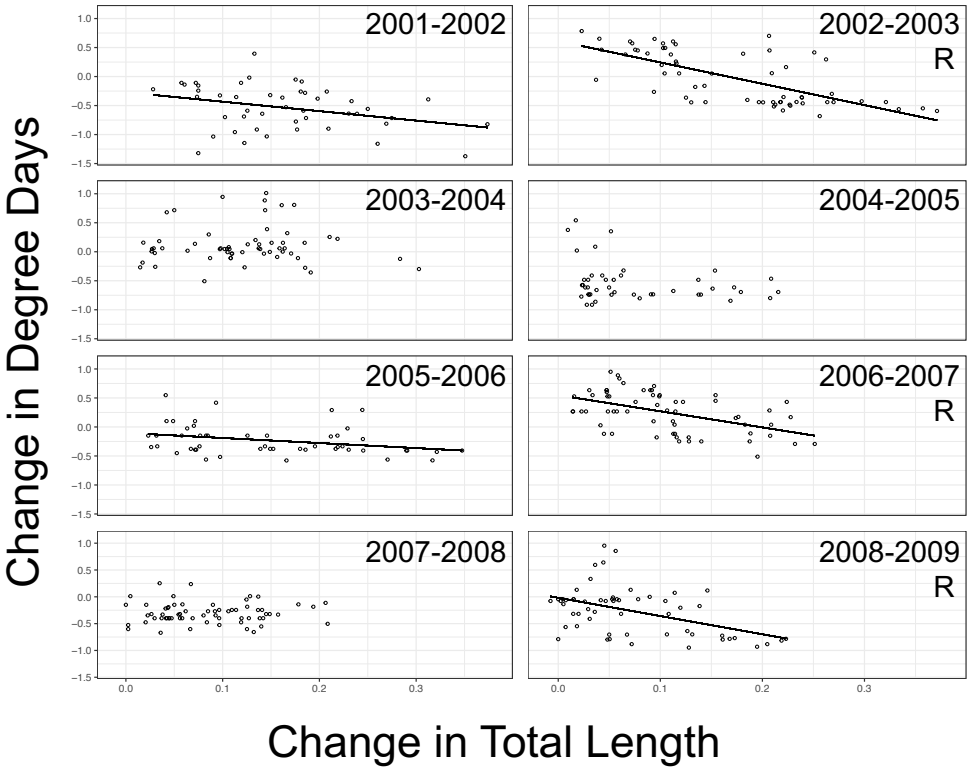
672

673 **Figure 1.**



674

675 **Figure 2.**


2001-2002
2002-2003
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Change in Degree Days
Change in Total Length

Figure 3.