

Condition-dependent reproductive tactics in male smallmouth bass: evidence of an inconsistent birthdate effect on early growth and age at first reproduction

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Keywords

alternative reproductive tactics; birthdate effect; conditional strategy; life history; *Micropterus dolomieu*; smallmouth bass; growth; body size.

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Editor: Jean-Nicolas Volff

Received 15 June 2016; revised 2 December 2016; accepted 14 February 2017

doi:10.1111/jzo.12454

Abstract

Many animals exhibit alternative forms of reproductive behavior, the expression of which depends on individual condition or status. For instance, male smallmouth bass *Micropterus dolomieu* that are large early in life often build a nest and spawn for the first time at a young age and small body size, while males that are small early in life delay reproduction, invest in growth and spawn when they are older and larger, tactics referred to as α and β , respectively. The observation that larger males also tend to spawn earlier *within* a season led to a hypothesis that birthdate – more specifically, dispersal date – may control which tactic is adopted. Here, we examined the individual growth and reproductive histories of 184 male *M. dolomieu* of three cohorts for evidence of a birthdate effect on early life condition and the subsequent expression of tactics, namely whether a long first-year growth period tends to induce the α tactic and whether variability in the timing of reproduction by parents within a season contributes to body size differences in progeny at the end of their first-year growth period. The extent to which male condition early in life influences the expression of tactics was also evaluated. Evidence of a birthdate effect on progeny condition and subsequent tactic choice was observed for only one of the three cohorts and, in another cohort, tactic choice and individual condition were largely unrelated. The seasonal variability in birthdates and growth histories suggest that a broad range of swim-up dates may be necessary to generate differences in condition early in life that are sufficiently large to control future reproductive decisions. Potential impacts of various physical, environmental and biotic factors that may mediate the seasonal timing of reproduction by parents or individual growth early in life are discussed.

Introduction

In many animal populations individuals exhibit discrete, alternative forms of reproductive behavior (reviewed by Gross, 1996; Shuster & Wade, 2003; Taborsky, Oliveira & Brockmann, 2008). The expression of alternative tactics has been of particular interest because the fitness of an individual often depends on which tactic is adopted. Gross & Repka (1998) showed, rather surprisingly, that it is possible for alternative tactics to be in a stable equilibrium when tactics are inherited and yield unequal fitness (see also Hazel, Smock & Lively, 2004). Their model, called the *conditional strategy*, is founded

on the idea that a genetic mechanism directs individuals into specific life history pathways based on their condition or status such that status-dependent fitness is maximized.

Individual condition and, hence, the expression of tactics can be influenced by a variety of non-genetic factors, like early life experiences or maternal or paternal effects, which are ubiquitous in natural populations (reviewed by Bernardo, 1996; Emlen, 2008). The condition or behavior of parents may, for instance, determine the condition of their progeny and, thereby, indirectly control the expression of progeny tactics. Wiegmann *et al.* (2004) revised the conditional strategy model and showed that tactic frequencies can be evolutionarily stable even

when tactic fitness is unequal and such non-genetic influences cause tactics to alternate across generations. Indeed, several mechanisms that produce a generational alternation of tactics have been identified (Bilton, 1971; Tsukamoto *et al.*, 1987; Janssen *et al.*, 1988).

Wiegmann *et al.* (2004) applied their revised model to a population of smallmouth bass (*Micropterus dolomieu*) in which differences in male condition – specifically, body size – early in life were conjectured to induce a generational alternation of tactics (Baylis, Wiegmann & Hoff, 1993; Wiegmann, Baylis & Hoff, 1997). From life tables they showed that nearly half of the males in a cohort of their study population might follow such a tactic trajectory. The hypothesized cause of variation in early-life condition, which directs males into alternative tactics, is a birthdate effect (*sensu* Taborsky, 1998). Birthdate is expected to exert some level of control over tactic expression, albeit indirect, when reproduction is seasonal, growth is indeterminate – so that early-born individuals tend to be larger – and an ontogenetic trait, like body size, functions as a proximate cue for tactic choices. Thus, it is perhaps no surprise that a birthdate effect has been implicated in the control of tactic choices in several fishes (Kodric-Brown, 1986; Magnhagen, 1992; Pastres *et al.*, 2002; Fagundes *et al.*, 2015). There is also good evidence that such an effect causes tactics to alternate across generations in ayu (*Plecoglossus altivelis*) (Tsukamoto *et al.*, 1987). Evidence that the reproductive tactics of *M. dolomieu* are influenced by birthdate has, however, not been documented.

In this study, we examined the individual growth and reproductive histories of 184 males from three cohorts in a different population of *M. dolomieu* for evidence of the hypothesized birthdate effect on the conditional expression of tactics. In the next section of the paper, we provide an overview of *M. dolomieu* reproductive behavior and describe how a

birthdate effect is hypothesized to cause differences in condition early in life and, thereby, control tactic choices. The specific predictions that we evaluated are also detailed.

Hypothesized birthdate effect and tactic expression

In northern populations, male *M. dolomieu* build nests and spawn in the spring between water temperatures of 15–20°C. Typically, male *M. dolomieu* mate monogamously and sneakers have never been observed (Ridgway, Goff & Keenleyside, 1989; Wiegmann, Baylis & Hoff, 1992). Importantly, energetic constraints – smaller males emerge from winter with a proportionately higher energy deficit than larger males – or competition forces smaller males to spawn later in a season than larger males (Ridgway, Shuter & Post, 1991; Baylis *et al.*, 1993; Mackereth, Noakes & Ridgway, 1999).

Parental care is paternal and males guard nests for a week or longer until fry swim up and disperse (Gross & Kapuscinski, 1997; Ridgway *et al.*, 2002). Progeny in nests of larger males often develop more slowly than the progeny of smaller males – because larger males initiate reproduction at cooler water temperatures – but typically disperse earlier (Ridgway & Friesen, 1992). Progeny feed and grow into the fall and, when the water temperature drops below 7–10°C, presumably find shelter in the littoral zone, where they over winter in a state of torpor (Suski & Ridgway, 2009). Thus, the progeny of large males, born earlier in a season, are expected to experience a longer growth period and to be larger at the end of their first year than progeny of smaller males, born later in a season (Shuter *et al.*, 1980; Goodgame & Miranda, 1993).

Figure 1 illustrates how tactic alternation is hypothesized to arise from a birthdate effect on the early-life condition of male

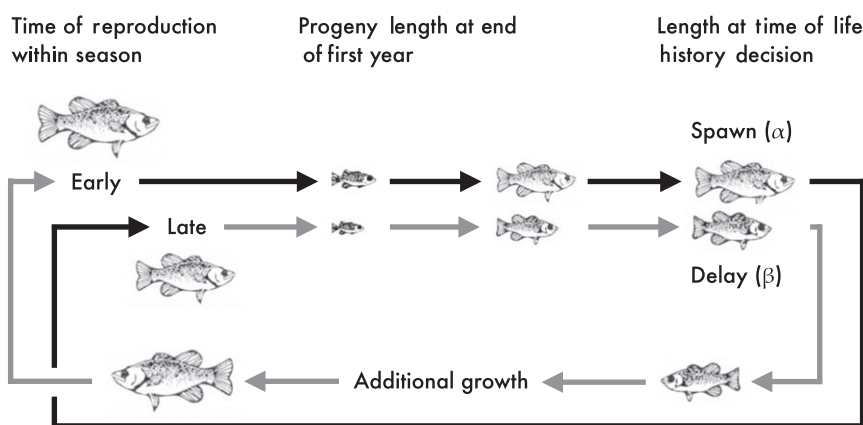


Figure 1 Hypothesized birthdate effect on age at first reproduction and the alternation of tactics across generations in male *M. dolomieu*. Body size differences early in life are presumably perpetuated and dictate the age at which males first spawn and body size at the age of reproduction determines when, within a season, reproduction is initiated. In particular, males that are large early in life spawn for the first time at a young age and relatively small body size, while males that are small early in life invest in growth and spawn when they are older and larger, tactics referred to as α and β , respectively. Because β males invest in growth they are larger than α males at the age of first reproduction so that α and β males from the same cohort spawn, respectively, late and early within the season that reproduction is initiated. Thus, the progeny of α males, born late within a season, have a short first-year growth period, whereas the progeny of β males, born early within a season, experience a longer first-year growth period. This birthdate effect is hypothesized to produce differences of progeny body size early in life that dictate tactic choices and cause tactics to alternate across generations. Adapted from Wiegmann *et al.* (1997).

progeny. The tactics, called α and β , indicate the age and body size of a male when reproduction is initiated, where α males spawn at a young age and small body size and β males spawn when they are older and larger (Wiegmann *et al.*, 2004). The key assumptions are that birthdate differences, which delimit the length of the first-year growth period, affect body size differences such that the progeny of α males are smaller than the progeny of β males at the end of the first year of life; body size early in life controls future reproductive decisions, where males that are large *at the end of their first year* tend to adopt the α tactic; and males that delay reproduction and first spawn when they are older – that is, adopt the β tactic – invest in growth and are relatively large when reproduction is initiated. The first assumption has not been directly evaluated, but in Jones Bay, Lake Opeongo, Ontario – perhaps the best-studied population of *M. dolomieu* – a single-season study revealed no clear relationship between dispersal dates and juvenile body size in the fall (Ridgway *et al.*, 2002). The second and third assumptions are largely supported in studies of *M. dolomieu*, but in Jones Bay the second assumption does not appear to be upheld (Wiegmann *et al.*, 1997, 2004; Dunlop, Shuter & Ridgway, 2005).

In this paper, we examined the growth and reproductive histories of 184 males of three cohorts to evaluate two predictions derived from the hypothesized birthdate effect, namely that a long first-year growth period should induce a high proportion of the α tactic and that the range of days over which fry disperse from nests within a season should be positively related to the variability in juvenile body size at the end of the first-year growth period. In addition, we determined whether males that adopted the α tactic were larger after their first year than β males – that is, whether tactic choice was contingent on early-life condition – and whether β males spawned for the first time at a larger body size than α males, a condition required for the alternation of tactics across generations.

Materials and methods

Study site

This study was conducted on Palette Lake, a 70-ha research lake in the Northern Highlands Fishery Research Area of north-central Wisconsin (46.067 N, –89.604 W). Saunders *et al.* (2002) describe its benthic and limnological characteristics. The lake is managed by the Wisconsin Department of Natural Resources. In the course of this study, a 40.6 cm total length minimum size limit was in effect and enforced by a mandatory creel census, which precluded the legal harvest of any *M. dolomieu* of the lengths included in our sample (Newman and Hoff 2000). The field methods we used follow those described in detail in papers on the population of *M. dolomieu* in Nebish Lake, a nearby lake in the Northern Highlands Fishery Research Area (46.052 N, –89.591 W; Raffetto, Baylis & Serns, 1990; Wiegmann *et al.*, 1992, 1997, 2004; Wiegmann & Baylis, 1995; see also Saunders *et al.*, 2002).

Nest census

Palette lake was surveyed daily in May, June and early July by snorkelers and observers in boats to census parental males in 2000–2007. The dispersal – swim-up – dates of fry were recorded to determine the end of a reproductive season and the start of the first year growth period for progeny.

Sample of males

Parental males were captured from nests and their total lengths (mm) were measured. Individuals were marked with Floy FD-67C anchor tags for future identification and scales were collected. Individuals were subsequently released. The males included in this study were individuals of the 2000, 2001 and 2002 cohorts that spawned for the first time in 2002–2007. In each year, we attempted to capture all males in the lake that successfully mated. Importantly, any bias introduced by tag loss or missed first-time breeders due, say, to nest abandonment should lead to *less* support for our model, as such events would tend to blur any relationship between growth histories and reproductive decisions.

Growth histories

Digital images of scales were used to age males and to determine growth histories. Focus-to-annulus and focus-to-margin distances were measured with ImageJ 1.37 at calibrated magnifications of 16 $\times$, 20 $\times$ or 40 $\times$ (Abramoff *et al.*, 2004). The Fraser-Lee growth model, with a correction factor of 35 mm, was used to back calculate the total length of an individual when each annulus was established (reviewed by Pierce, Rasmussen & Leggett, 1996). This model, with the 35 mm correction factor, was verified for *M. dolomieu* in Nebish Lake (Klumb, Bozek & Frie, 1999).

The first-year growth period for a cohort was estimated as a range based on swim-up dates and water temperature at a depth of approximately 1 m. In particular, the lower (upper) bound of the growth period was computed as the interval (days) between the last (first) observed swim-up date and the day on which the mean daily water temperature dropped below 10°C (Appendix S1). In addition, the number of degree-days accumulated over the growth period, a measure of thermal history that is often a good predictor of development and growth rate in fishes and other organisms, was computed as the sum of positive differences between the mean daily water temperature and the threshold 10°C (reviewed by Neuheimer & Taggart, 2007).

Statistical analyses

A χ^2 test was used to determine if the proportions of males that initiated reproduction at specific ages varied amongst the cohorts. A Bartlett test was used to compare the variances of age-specific body size amongst males of the three cohorts, followed, where appropriate, by pairwise *F* tests to identify which of the variances differed. A Welch ANOVA, which allows for unequal within-group variances, was used to compare the mean age-specific total lengths of males across cohorts, followed,

when appropriate, by pairwise *t* tests (unequal variances assumed) to determine which means differed (Myers & Well, 2003).

Analysis of variance was used to compare age-specific lengths of males that first spawned at different ages *within* each cohort and, in particular, to determine whether body size early in life was related to the age at which reproduction was initiated. A significant ANOVA was followed by pairwise Fisher Least Significant Difference (FLSD) *t* tests to identify which of the age-specific mean total lengths differed. Likewise, ANOVA and FLSD *t* tests were used to evaluate whether males of a cohort that delayed reproduction – that is, adopted the β tactic – spawned for the first time at a larger body size than males that adopted the α tactic. A significance level of $\alpha = 0.05$ was used for all tests and results were interpreted with respect to the length of the first-year growth period, and the degree days accumulated over this period, for males of the 2000, 2001 and 2002 cohorts.

Results

In 2000, 2001 and 2002 fry dispersed from nests over a period of 14 days (6–19 June, 2000), 28 days (1–28 June, 2001) and 16 days (14–29 June, 2002). These dispersal dates bounded growth periods that spanned 143–156 days, 119–146 days and 115–130 days. The three cohorts experienced 1225–1343, 1190–1431 and 1266–1413 degree-days, or a range of 118, 241 and 148 degree-days, over this period, respectively (Fig. 2).

A total of 43, 109 and 32 males of the three cohorts spawned for the first time in 2002–2007. The proportion of males that initiated reproduction at ages 2–5 years differed significantly amongst the cohorts (Table 1). The majority of males in each cohort spawned for the first time at an age of 3–4 years. However, males tended to spawn at a younger age if a cohort experienced a longer first-year growth period. The 2000 cohort experienced the longest growth period – as long as 156 days – and 26% of males first spawned at age 2 years. The 2001 cohort experienced an intermediate growth period – as long as 146 days – and 17% of males spawned at age 2 years. The 2002 cohort experienced the shortest growth period – not longer than 130 days – and only 3% of males first spawned at age 2 years. Interestingly, a single male of the 2002 cohort also delayed reproduction until age 5 years.

The age-specific total lengths and reproductive decisions for males of the three cohorts are summarized in Table 2. The mean body size of males of the three cohorts at the end of their first year of life did not differ (Welch ANOVA, $F_{2,89,21} = 0.79$, $P = 0.4588$). The variance of total length at the end of the first growth period, however, differed amongst the cohorts (Bartlett $X^2_2 = 18.27$, $P = 0.0002$). The variances were, as predicted, roughly proportional to the range of birthdates – more specifically, the dates over which fry dispersed from nests – and cohort differences in first-year thermal history. The variance of total length was 40 mm² and 34 mm² for males of the 2000 and 2002 cohorts, which dispersed from nests over 14–16 days and experienced a range of 118–148 degree-days before winter. These variances do not differ from

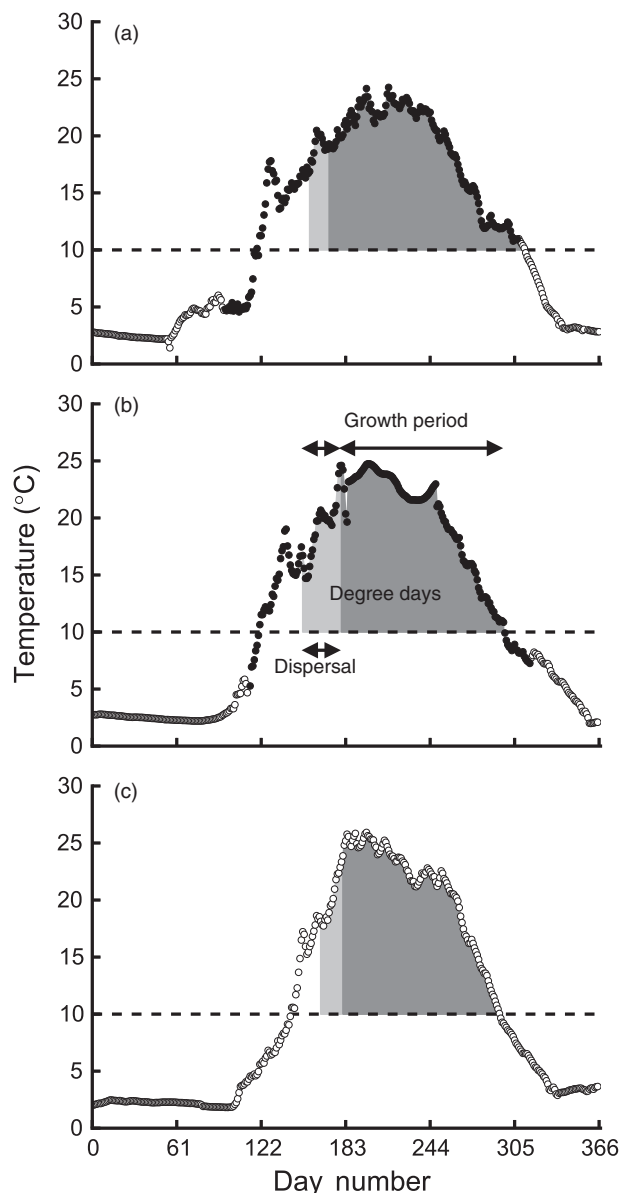


Figure 2 First-year growth period and degree-days experienced by progeny that dispersed from nests in (a) 2000, (b) 2001 and (c) 2002. The lightly shaded areas delineate the range of dispersal dates: 6–19 June, 1–28 June and 14–29 June in 2000, 2001 and 2002. The degree-days experienced in the first year of life correspond to the shaded areas between the temperature profile and 10°C (horizontal, dashed lines). The cohorts experienced 1225–1343, 1190–1431, 1266–1413 degree days over a growth period – the number of days between the start or endpoint dispersal date and the date on which the mean water temperature dropped under 10°C – that lasted 143–156, 119–146 and 115–130 days. Filled circles correspond to water temperatures measured in Pallette Lake and open circles to water temperatures that were estimated (Appendix S1).

one another ($F_{31,42} = 1.19$, $P = 0.3128$). Fry dispersed from nests over a period of 29 days and experienced a range of 241 degree-days before winter in 2001. The variance of total length

Table 1 Number (proportion) of males of the 2000, 2001 and 2002 cohorts that first spawned at age 2–5 years

Cohort	Age at First Reproduction ^a				Total
	2	3	4	5	
2000	11 (0.26)	22 (0.51)	10 (0.23)	0 (0.00)	43
2001	18 (0.17)	77 (0.71)	14 (0.13)	0 (0.00)	109
2002	1 (0.03)	26 (0.81)	4 (0.13)	1 (0.03)	32

^aThe proportion of males that first spawned at age 2, 3 or 4 years differed significantly amongst the cohorts ($\chi^2_4 = 10.9$, $P = 0.0282$). (The 5-year-old category was excluded from this statistical test to avoid cell expectations of less than five individuals.)

amongst males of the 2001 cohort at age 1 year was 97 mm², significantly larger than the variance amongst males in the cohort of 2000 ($F_{42,108} = 2.43$, $P = 0.0008$) or 2002 ($F_{31,108} = 2.88$, $P = 0.0006$).

Table 2 reveals that males of the 2000 and 2001 cohorts that reached a mean total length of approximately 200 mm by their second year spawned at age 2 years and that at any particular age the largest males spawned. Examination of growth histories reveals, however, that tactic choice by males of the 2000 cohort was not related to body size differences at the end of the first-year growth period (Fig. 3). Instead, the growth histories imply that growth rate between age i and $i + 1$ – not an initial size advantage – triggered the decision to spawn at age $i + 1$. The growth histories for males of the 2001 cohort, in contrast, reveal that the birthdate-induced variability in early life condition had a subsequent influence on tactic decisions: length differences at age 1 year were perpetuated and indicative of the age at which males first spawned. In particular, the largest males at age 1 year tended to spawn

for the first time earlier in life than smaller individuals. Neither growth rate nor body size (at any age) was indicative of the age at which males of the 2002 cohort first spawned. Table 2 also reveals that, generally, the longer males delayed reproduction the larger they were when they first spawned, as is required for the alternation of the two tactics across generations.

Discussion

The growth histories and schedules of reproduction for males of the three cohorts reveal an inconsistent effect of birthdate on progeny condition and subsequent reproductive decisions. In 2000 and 2001 fry dispersed from nests early and experienced a long first-year growth period – early birthdates – in comparison to 2002 and a relatively high proportion of males of the 2000 and 2001 cohorts spawned at a young age (Table 1). Fry in 2001 dispersed from nests over 29 days, a period nearly twice as long as in 2000 or 2002. The range of their thermal histories was likewise broad and their body size at the end of the first year of life varied more than that for males of the other two cohorts. Thus, the variability in birthdates within a season also induces, in some years, notable body size differences in male progeny at the end of their first growth period.

The growth histories also reveal evidence for the condition-dependence of reproductive decisions. In particular, males of the 2000 and 2001 cohorts that were large at any particular age spawned while small males delayed reproduction until they were older and, generally, larger, a pattern observed in other populations (Wiegmann *et al.*, 1997; Dunlop *et al.*, 2005). For males of the 2000 cohort rapid growth between age i and $i + 1$ appears to have favored a decision to spawn at age

Table 2 Reproductive decisions and cross-cohort comparisons of male age-specific total lengths (mm). Total sample sizes and the number of males that spawned or delayed reproduction at each age are given in parentheses. The age-specific variance of total length for each cohort is shown in brackets

Cohort	Decision	Male age				
		1	2	3	4	5
2000	Spawn		200.7 ^a (11)	278.4 ^a (22)	273.4 ^a (10)	
	Delay		164.3 ^b (32)	221.9 ^c (10)		
	Total	73.7 ^A (43) [40.0] ^B	173.6 ^A (43) [601.5] ^A	260.8 ^A (32) [940.4] ^A	273.4 ^A (10) [925.3] ^A	
2001	Spawn		202.9 ^a (18)	245.5 ^b (77)	269.9 ^a (14)	
	Delay		143.7 ^c (91)	191.1 ^d (14)		
	Total	74.2 ^A (109) [97.1] ^A	153.5 ^B (109) [852.8] ^A	237.1 ^B (91) [858.4] ^A	269.9 ^A (14) [192.9] ^B	
2002	Spawn		167.9 (1)	227.2 ^c (26)	301.65 ^b (4)	303.2 (1)
	Delay		143.3 ^c (31)	228.0 ^{bc} (5)	242.1 (1)	
	Total	75.5 ^A (32) [33.8] ^B	144.1 ^B (32) [265.1] ^B	227.4 ^B (31) [321.8] ^B	289.7 ^A (5) [897.5] ^A	303.2 (1) [0]

Different superscript capital letters (A, B) indicate a significant difference of mean [variance] age-specific total length between cohorts and different superscript lowercase letters (a, b, c, d) indicate differences in mean total length between and within cohorts in relation to individual reproductive decisions. All contrasts labeled with letters correspond to comparisons within age columns. The mean body size of males of a cohort at the age of first reproduction corresponds to the row labeled *Spawn* and all means within a row differ significantly except between males of the 2000 cohort that first spawned at age 3 or 4 years (cells shaded). Groups with a sample size of one (1) were excluded from formal analyses.

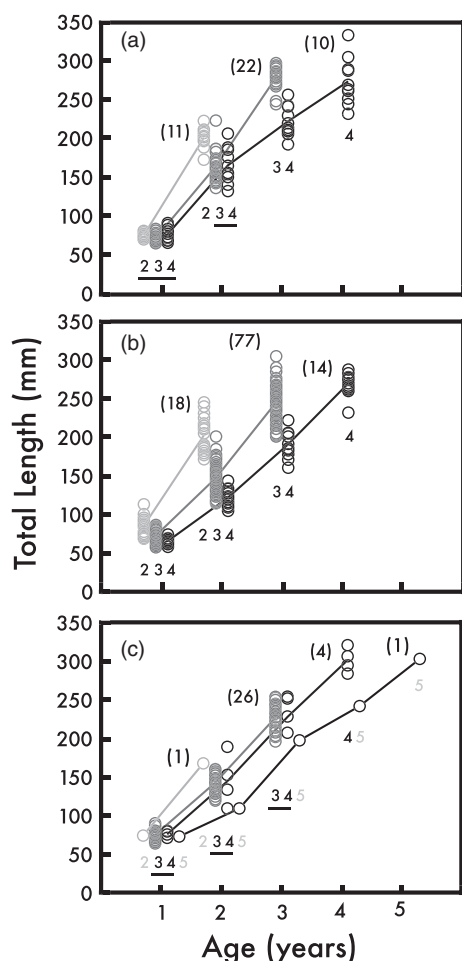


Figure 3 Individual growth histories for males of the (a) 2000, (b) 2001 and (c) 2002 cohorts. Numbers 2, 3, 4 and 5 under growth curves indicate the age at which males of a cohort first spawned. Numbers are underlined if age-specific total lengths did not differ significantly. Sample sizes are indicated in parentheses. (The singleton males of the 2002 cohort that spawned for the first time at age 2 or 5 years were excluded from comparisons.)

$i + 1$. In principle, a birthdate effect can exert its influence at any stage of ontogeny, but patterns of growth for males of the 2000 cohort provide no obvious link to a birthdate effect (Fig. 3). The growth histories for males of the 2001 cohort, in contrast, display the critical, hypothesized tie between body size differences at the end of the first growth period and tactic choices. Indeed, the 2001 cohort provides the strongest evidence in support of the hypothesized birthdate effect on individual reproductive decisions.

In 2000 and 2002 fry dispersed from nests over 14–16 days, as compared to 29 days in 2001, and the body size of males in these two cohorts at the end of their first year of life was relatively invariant and unrelated to the age at which they first spawned. Thus, a broad range of swim-up dates appears to be necessary to induce differences in progeny condition early in life that are sufficiently large to control future reproductive decisions. Indeed, in higher latitude *M. dolomieu* populations

weather conditions may compress dispersal dates and disassociate birthdate from juvenile condition at the end of their first year (Ridgway *et al.*, 2002). In Lake Opeongo, Ontario, for instance, *growth rate* appears to determine the age at which males first spawn and in another nearby Ontario lake age at first reproduction is largely unrelated to growth rate or body size at any particular age (Dunlop *et al.*, 2005). The 2000 and 2002 cohorts in Pallette Lake displayed similar patterns (Fig. 3). The relationship may also be decoupled by severe winters that induce high mortality amongst small individuals and, thereby, truncate body size variability generated by variability in dates of dispersal (Garvey, Ostrand & Wahl, 2004). These considerations imply that birthdate effects on progeny condition and tactic frequencies probably vary, like other life history characters, on a latitudinal gradient (reviewed by Conover, Duffy & Hice, 2009).

Wiegmann *et al.* (2004) estimated that a large proportion of male *M. dolomieu* could be involved in a generational alternation of tactics in nearby Nebish Lake, whereas in Pallette Lake this process would appear to be limited. Thus, conditions other than weather, like physical characteristics of lakes – particularly, attributes that influence the rate at which the water temperature changes in the spring or fall – may also mediate birthdate effects on progeny status. The impact of a birthdate effect is probably also sensitive to the temporal dynamics of prey availability, which could augment or diminish body size differences induced by differences in birthdates (Ludsin & DeVries, 1997; Pine, Ludsin & DeVries, 2000; Garvey, Herra & Leggett, 2002). Population density, predation and regulations on anglers, which can induce complex patterns of energy allocation, growth and maturation, seem also likely to influence tactic decisions (Jørgensen & Fiksen, 2010; Ivan & Höök, 2015). Indeed, the density of *M. dolomieu* in Nebish Lake is considerably higher than in Pallette Lake and the two lakes have experienced a vastly different fishery management (Hoff & Serns, 1990; Hoff, 1995; Newman and Hoff 2000). Lastly, the degree to which populations exhibit iteroparity – higher in Pallette Lake than Nebish Lake – is expected to alter tactic dynamics because males that first spawn at a young age and live to reproduce again later are expected to grow and, in their second and subsequent seasons, spawn earlier so that their sons are likely to be large, as they themselves were, at the end of the first year growth period.

How tactic choices are controlled has special implications for the evolutionary dynamics of populations (Beckerman *et al.*, 2002; Benton *et al.*, 2005; Wright & Gibb, 2005). Many temperate fishes, like bluegill sunfish (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*), exhibit size-dependent patterns of reproduction similar to those of *M. dolomieu* (reviewed by Neff & Knapp, 2009). These species also exhibit protracted episodes of reproduction and, quite often, there is a notable birthdate effect on the body size of progeny (Miller & Storck, 1984; Phillips, Jackson & Noble, 1995; Cargnelli & Gross, 1996; Ludsin & DeVries, 1997; Garvey *et al.*, 2002; Cargnelli & Neff, 2006). The influence of birthdate on tactic choices and the possibility of tactic alternation in other fishes, it seems, could be fruitfully explored.

Acknowledgments

For helpful hands in the field we thank S. Bassak, R. Cox, K. Deem, C. Freund, N. Frisch Welch, M. Healey-McNamara, A. Johnson, A. Kautza, K. Kouns, D. Logan, D. Lubin, M. Rice, B. Saetre, V. Schwantes, B. Shefveld, R. Thoni, L. Trayber, J. van Schyndel, K. Weinersmith, J. Weiss, K. Wernert and P. White. The University of Wisconsin Trout Lake Biological Station provided logistical support and accommodations, for which we are grateful. R. Saunders kindly provided us with swim-up dates for fry in 2000. Temperature data from Sparkling Lake were obtained from the North Temperate Lakes Long Term Ecological Research website (<https://lter.limnology.wisc.edu>). Lastly, we thank M. Taborsky and three anonymous reviewers for helpful comments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Mean daily water temperature calculations for 2000, 2001, and 2002.