Variation in Reproductive Life History Traits between Two Populations of Blackbanded Darters (*Percina nigrofasciata*)

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We examined the life history of Blackbanded Darters (*Percina nigrofasciata*) from two streams in the Choctawhatchee River drainage, Florida, over a three-year study period. Blackbanded Darters from Turkey Creek were longer than fish from Ten Mile Creek; however, size-adjusted clutch and egg sizes were similar between populations. Larger females produced larger clutches, whereas egg size did not vary with female body size. Seasonally, clutch sizes were greater in May than in August. When contrasted with previous studies of Blackbanded Darters in Alabama and Louisiana, the reproductive season of Blackbanded Darters in Florida was unusually long, ceasing for only a few months in late fall. The reproductive season was longer in Turkey Creek than in Ten Mile Creek. Differences in thermal regime among streams may explain differences in life history traits among local and distant populations of Blackbanded Darters. This research, alone and in combination with previous studies of this species, emphasizes two main points. First, it reaffirms that life history studies based on a single locality or conducted at a single point in time may fail to capture the full range of variation in life history traits. Second, it highlights the extensive phenotypic variation found in species with broad geographic ranges. Such species lend themselves to comparative and experimental research on patterns and causes of life history variation.

A general aim of life history studies is to identify spatial and temporal patterns of variation in life history traits and to understand the underlying causes of variation among populations and species. Life histories represent adaptations to environmental conditions experienced by populations over time (Roff, 1992; Stearns, 1992). Measuring and characterizing variation in life history traits, therefore, enhances our understanding of the selective pressures faced by different populations as well as constraints on their ability to respond adaptively to these pressures.

North American darters (Perciformes: Percidae) commonly exhibit spatial and temporal variation in reproductive traits. Body size, duration of spawning season, clutch size, and egg size vary within and among populations for many species (Heins and Rooks, 1984; Marsh, 1984; Hubbs, 1985; Heins and Baker, 1989; Parrish et al., 1991; Heins and Machado, 1993; Guill and Heins, 1996, 2000; Heins, 2001; Heins et al., 2004). Comparative studies of a species across its range facilitate a more comprehensive understanding of ecological variation, especially of populations in different habitats.

In this study, we describe the reproductive life history of two populations of Blackbanded Darters (*Percina nigrofasciata*; Agassiz, 1854) in northwestern Florida and compare our findings to previous studies of this species from other portions of its range. Blackbanded Darters are widely distributed across the southeastern United States (Lee et al., 1980), are often locally abundant, and, unlike many other North American darters, their conservation status is currently stable (Page, 1983; Kuehne and Barbour, 1984; Warren et al., 2000; Jelks et al., 2008). Blackbanded Darters are therefore a model species for studying patterns and causes of life history variation in stream fishes.

MATERIALS AND METHODS

Study sites.—Our study sites on Turkey Creek (30.66844°N, 86.56308°W) and its tributary Ten Mile Creek (30.60125°N, 86.65853°W) are located approximately 8 km apart and flow through similar landscapes dominated by longleaf pine, wiregrass, and red oak vegetation on Eglin Air Force Base in Okaloosa County, Florida, USA. Although both streams are seepage-fed and sub-stenothermal, analysis of hourly water temperature data available from January to mid-June 1997 indicates that Turkey Creek is warmer and more thermally stable than Ten Mile creek (16.2–22.2, 19.6 ± 0.9 versus 9.2–24.4, 18.2 ± 2.8°C, range, mean ± 1 SE; paired t-test, t_{164} = 9.3, $P < 0.0001$). Additionally, Turkey Creek is wider (8.9 ± 0.1 versus 7.2 ± 0.1 m), deeper (71.0 ± 1.5 versus 58.5 ± 1.3 cm), and has a greater discharge rate (2.5 ± 0.1 versus 1.4 ± 0.1 m³/s) than Ten Mile Creek. Streambeds are principally quartzite sand interrupted by patches of coarse woody debris, whereas stream margins are lined with dense root mats, detritus, and submerged aquatic vegetation.

Fish collections.—We collected Blackbanded Darters in May, August, and November 1999; May and August 2000; and monthly from February 2001 to January 2002. During each collection, we measured water temperature to the nearest 0.1°C. About 30 Blackbanded Darters were collected from ≈200 m reaches within each creek during each sampling period for a total of 687 males and 396 females. Individual fish were located while snorkeling throughout a reach and chased into 4 mm mesh dip nets. Visual detection and manual collection of benthic darters is an effective method of capture across the range of habitats and conditions encountered in Turkey and Ten Mile creeks (Jordan et al., 2008). Blackbanded Darters occupy a wide variety of

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substrates found in streams (Suttkus and Ramsey, 1967; Mathur, 1973; Henry and Grossman, 2008); in our study, Blackbanded Darters mostly occurred on open sandy bottoms in the stream channel or were perched on logs or vegetation along stream margins. To avoid sampling bias, we aimed to capture every individual we encountered. Fish were immediately preserved and stored in 10% buffered formalin. All specimens were deposited in Tulane's Museum of Natural History fish collection (Catalog #194747–194780).

Quantification of life history parameters.—Standard length (SL) of each fish was measured to the nearest 0.01 mm using digital calipers. Eviscerated fish were blotted dry and weighed to the nearest 0.001 g to determine body mass. Gonads were isolated to determine sex, to assess reproductive stage, and to quantify clutch parameters. Intact gonads from all fish were blotted dry and weighed to the nearest 0.001 g. Males were categorized as either latent or mature based on the appearance of testes. Latent testes were small, thin, and transparent to translucent. Mature testes were opaque and grainy in appearance, and, as size increased, often became convoluted and triangular in cross-section. Females were classified into one of six stages: latent, early maturing, late maturing, mature, mature-ripening, or ripe. Female classifications are part of the seasonal clutch production cycle and are based on coloration, size, and position of oocytes and eggs in ovaries, as described by Heins et al. (1992) and Heins and Baker (1993a).

We evaluated the percentage of females with clutches of eggs from each collection. Only mature, mature-ripening, and ripe females contained distinct clutches, evident as a group of larger oocytes or eggs (Heins and Baker, 1993a). Ovaries of clutch-bearing females were dissected. In mature and mature-ripening females, clutch oocytes were separated from surrounding immature oocytes and follicular material. In ripe females, eggs in the clutch were concentrated in the lumens of the ovaries. Oocytes or eggs comprising a clutch in mature and mature-ripening females were counted to determine clutch size. Ripe females may have already oviposited some of their eggs (Heins and Baker, 1993a) and were not used for clutch counts. Clutches were dried at 40°C for 24 hours and weighed to the nearest 0.0001 g. We calculated mean oocyte or egg mass by dividing dry clutch mass by the number of oocytes or eggs in the clutch.

We considered standard length of the smallest mature male and clutch-bearing female as the minimum size of reproductive maturity for males and females, respectively. We calculated average reproductive size from the arithmetic mean of standard length for all mature, mature-ripening, and ripe females and for all mature males.

Statistical analyses.—Continuous variables were $\log_{10}$-transformed prior to parametric analyses. We used log-likelihood ratio chi-square tests to compare the observed sex ratio to an expected ratio of 1:1 and to test for effects of creek and sampling period on sex ratios. We used logistic regression to determine if body size was related to sex. We used analysis of variance or analysis of covariance to test for effects of creek, sex, and sampling period on life history traits (standard length, eviscerated weight, gonad weight, clutch size, egg mass). Standard length was included as a covariate for analyses of eviscerated weight, gonad weight, clutch size, and egg mass, because body size is often correlated with these other life history traits (Roff, 1992; Stearns, 1992). We used Tukey's HSD *post-hoc* test to compare egg size or clutch size following a significant F-test. Boundaries of the reproductive season were determined by presence of the first and last reproductively mature males and clutch-bearing females across collections made between February 2001 and January 2002. To determine if there was seasonal variation in female size or clutch parameters (clutch size and egg mass), we used planned contrasts to compare least square means of fish collected in May of all three years to those collected in August.

Use of clutches from ripe females reduces estimates of clutch size because females may have released some ova prior to collection (Heins and Baker, 1993a, 1993b). Therefore, when testing for differences in clutch size, we used oocyte counts from mature and mature-ripening females only. Likewise, use of mature clutches may lead to underestimates of egg mass due to incomplete yolk loading in mature eggs (Heins et al., 1992). When testing for differences in ovum mass, we used oocyte mass of mature-ripening females and egg mass of ripe females only.

Analyses of transformed and untransformed data produced similar results, so we present descriptive statistics using untransformed data in order to simplify interpretation and facilitate comparison with published studies.

RESULTS

Size, maturity, and sex ratio.—Size of all males ranged from 17.5 to 95.3 mm SL (54.9 ± 0.6 mm; mean ± 1 SE), and all females ranged from 21.1 to 74.3 mm SL (46.0 ± 0.5 mm). The smallest reproductively mature male and female were 28.6 and 34.5 mm SL, respectively. Mean size of mature males was 62.8 ± 0.64 mm SL ($n = 401$). Mean size of clutch-bearing females was 50.5 ± 0.55 mm SL ($n = 173$). The simple regression equation between standard length and total weight for all fish combined was $\log_{10}$weight $= -5.49 + 3.30*\log_{10}$length ($F_{1,1081} = 84683.4$, $P < 0.0001$, $R^2 = 99\%$).

Males were on average 19% longer than females ($F_{1,1062} = 89.3$, $P < 0.0001$), a difference that was consistent between creeks ($F_{1,1062} = 0.3$, $P = 0.5920$). After controlling for differences in standard length, eviscerated males and females weighed about the same ($F_{1,1061} = 1.9$, $P = 0.1693$). In general, fish from Turkey Creek were slightly longer (4%) than fish from Ten Mile Creek ($F_{1,1062} = 6.5$, $P = 0.0111$), but not heavier ($F_{1,1061} = 0.5$, $P = 0.4995$). This pattern was true for both males and females, as indicated by the lack of an interaction between sex and creek for either length ($F_{1,1061} = 0.3$, $P = 0.5920$) or eviscerated weight ($F_{1,1061} = 0.2$, $P = 0.6593$). Standard length ($F_{17,1062} = 89.3$, $P < 0.0001$; Fig. 1A–D) and eviscerated weight ($F_{17,1061} = 106.1$, $P < 0.0001$) varied among sampling periods. Fish collected in August did not differ in length from those collected in May (planned contrast; $F = 1.5$, $P = 0.2266$) but were significantly lighter in eviscerated weight (planned contrast; $F = 32.5$, $P < 0.001$).

The overall sex ratio of 37% females and 63% males deviated significantly from the 1:1 ratio expected in sexually reproducing populations ($\chi^2_{1,1082} = 79.2$, $P < 0.0001$). Sex ratios did not vary significantly between creeks ($\chi^2_{1,1082} = 0.5$, $P = 0.4729$) and were consistent across sampling periods (Cochran-Mantel-Haenszel test; $\chi^2_{1,1082} = 0.1$, $P = 0.7629$). The probability that an individual was male increased with increasing standard length ($\chi^2_{1,1082} = 97.7$, $P < 0.0001$; Fig. 2). For example, 51% of fish 17–50 mm SL were male,
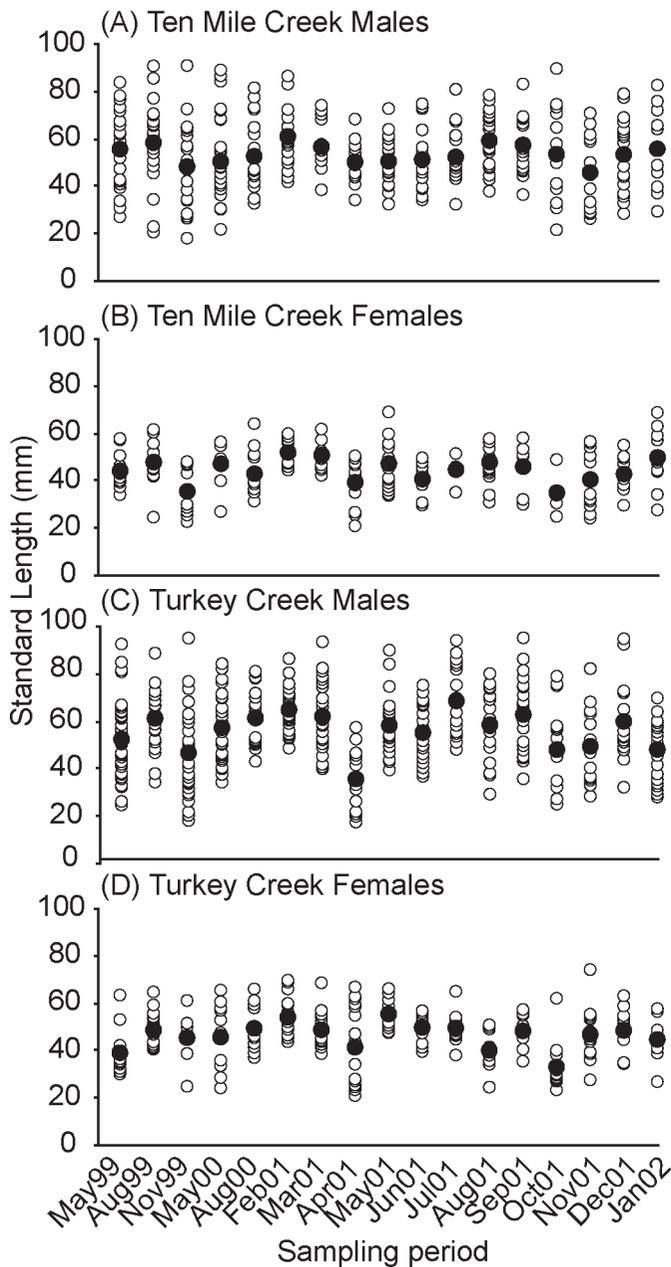
Fig. 1. Seasonal variation in standard length of Blackbanded Darters collected in northwestern Florida ($n = 1073$ individuals). (A) Males from Ten Mile Creek. (B) Females from Ten Mile Creek. (C) Males from Turkey Creek. (D) Females from Turkey Creek. Open circles represent individuals and closed circles indicate collection means.

Fig. 2. Relationship between sex ratio and standard length in Blackbanded Darters. Closed circles above the line indicate individual males and open circles below the line indicate individual females of a given size.

whereas 90% of fish 60–95 mm SL were male. Moreover, in the reproductively immature size class (all fish smaller than the minimum size of reproductive maturity), sex ratio was strongly biased toward females (67% female, 33% male; $\chi^2_{1,93} = 10.5$, $P = 0.0012$; Fig. 2).

Reproductive season.—We collected fish larger than the minimum reproductively mature size in every collection (Table 1). Mature males were present in each sampling period, but the percentage of reproductively mature individuals varied substantially (14–100%; Table 1). Overall, clutch-bearing females were present throughout the spring and summer but reproductive activity decreased during fall months (Table 1). Clutch-bearing females were collected in
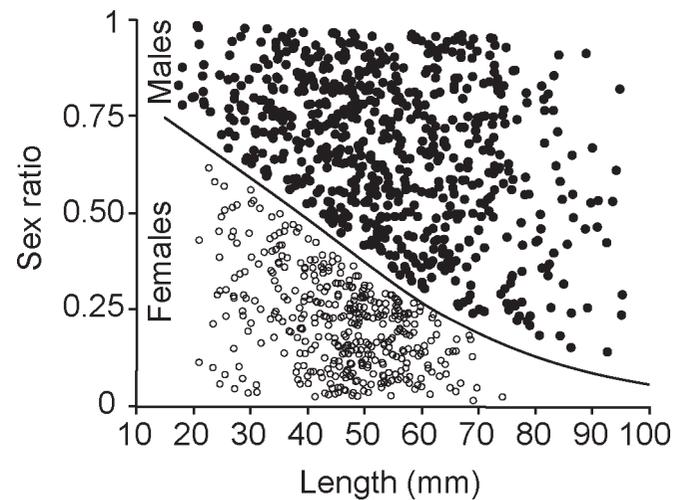
May and August of 1999 and 2000 but not in November 1999 (Table 1). In 2001, clutch-bearing females were collected in all months except October and November, although clutch production differed between the two creeks during the fall (Table 1). Females with clutches were present in every collection except October and November at Turkey Creek, whereas no clutch-bearing females were collected from September through December at Ten Mile Creek (Table 1).

Gonad weight.—Standard length explained 31 and 28% of the variation in gonad weight of males and females, respectively. Generally, larger males and females had larger quantities of gonadal tissue (females: $F_{1,312} = 175.9$, $P < 0.0001$; males: $F_{1,636} = 435.3$, $P < 0.0001$). Gonad size was similar between creeks (females: $F_{1,312} = 0$, $P = 0.9980$; males: $F_{1,636} = 0.2$, $P = 0.6479$), but differed among sampling periods (females $F_{17,156} = 12.9$, $P < 0.0001$; males $F_{17,636} = 15.5$, $P < 0.0001$; Fig. 3A, 3B). Both testes (planned contrast; $F = 46.5$, $P < 0.0001$) and ovaries (planned contrast; $F = 46.9$, $P < 0.0001$) were larger (i.e., heavier) in May than in August.

Clutch and egg size.—Clutch size (excluding ripe females) ranged from 4 to 73 eggs ($n = 159$, 26.5 ± 1.0 eggs). Standard length explained 36% of the variation in clutch size, with larger females generally producing larger clutches ($F_{1,142} = 110.3$, $P < 0.0001$; Fig. 4A). Clutch sizes were similar at the two creeks ($F_{1,142} = 0.9$, $P = 0.3383$) but differed among sampling periods ($F_{14,142} = 3.9$, $P < 0.0001$; Fig. 4B). For example, females from May produced clutches with 44% more eggs than females from August (planned contrast; $F = 4.1$, $P = 0.0449$).

Dry mass of individual eggs (excluding mature clutches) ranged from 547 to 984 µg ($n = 30$, 739 ± 20 µg). Eggs from mature clutches were significantly lighter than eggs from both ripening and ripe clutches ($F_{2,170} = 17.9$, $P < 0.0001$; Tukey's HSD *post hoc* $P < 0.05$). Larger females did not produce larger eggs than smaller females ($F_{1,16} = 2.4$, $P = 0.1385$; Fig. 5A). Egg masses were similar across all samples at both creeks ($F_{1,16} = 1.9$, $P = 0.1891$) but differed among sampling periods ($F_{11,16} = 4.8$, $P = 0.0024$; Fig. 5B). Between

Table 1. Seasonal Variation in Reproductive Status of Male and Female Blackbanded Darters Collected from Two Streams in Northwestern Florida. Temp is the water temperature at the time of collection (°C), RM is the number of individuals larger than the minimum size of reproductive maturity, and *n* is the number of individuals collected. Other values are percentages of individuals that were latent (LA) to early-maturing (EM), late-maturing (LM), mature (MA), mature-ripening (MR), and ripe (RE). Asterisks (*) indicate months when no clutch-bearing females were collected.

		Females				Female maturity stages			Males			
	Temp	RM	*n*	LA-EM	LM	MA	MR	RE	RM	*n*	LA	MA
Ten Mile												
May 99	20.7	12	12	25	0	67	0	8	21	24	33	67
Aug 99	23.6	15	16	44	6	50	0	0	19	21	33	67
Nov 99*	17.2	7	11	100	0	0	0	0	15	21	86	14
May 00	15.1	6	7	14	0	57	14	14	19	20	40	60
Aug 00	21.7	13	13	85	15	0	0	0	20	25	70	30
Feb 01	23.3	10	10	20	10	60	10	0	16	16	25	75
Mar 01	16.9	13	13	0	8	77	15	0	13	13	15	85
Apr 01	16.6	9	12	33	8	58	0	0	13	14	14	86
May 01	19.3	16	16	25	0	63	6	6	20	21	38	62
Jun 01	21	9	9	33	0	67	0	0	18	19	37	63
Jul 01	22.6	4	4	50	0	50	0	0	16	17	59	41
Aug 01	23.1	14	14	50	7	29	0	14	18	18	17	83
Sep 01*	22.7	8	8	100	0	0	0	0	17	17	35	65
Oct 01*	21.7	4	5	100	0	0	0	0	10	13	69	31
Nov 01*	19.2	9	11	100	0	0	0	0	9	14	71	29
Dec 01*	18.6	10	10	100	0	0	0	0	16	18	33	67
Jan 02	16.3	11	12	17	50	25	8	0	10	11	45	55
Turkey												
May 99	20.4	10	10	60	0	30	0	10	36	41	49	51
Aug 99	21.4	19	19	42	11	42	5	0	21	22	32	68
Nov 99*	19.3	6	7	100	0	0	0	0	23	33	76	24
May 00	20.7	10	10	46	15	38	0	0	24	24	36	64
Aug 00	21.3	11	13	60	20	0	10	10	24	25	21	79
Feb 01	19.2	20	20	0	20	65	10	5	26	26	0	100
Mar 01	19.1	16	16	6	13	63	19	0	30	30	20	80
Apr 01	19.9	9	16	50	6	31	6	6	8	16	63	38
May 01	20.5	11	11	0	0	55	9	36	20	20	60	40
Jun 01	21	10	10	10	10	80	0	0	20	20	50	50
Jul 01	21.2	13	13	38	0	54	8	0	20	20	35	65
Aug 01	21.1	10	11	73	0	18	0	9	18	19	16	84
Sep 01	20.7	8	8	88	0	13	0	0	22	22	27	73
Oct 01*	19.9	7	11	100	0	0	0	0	11	16	63	38
Nov 01*	19.7	15	16	93	7	0	0	0	12	14	50	50
Dec 01	19	14	14	73	7	20	0	0	14	15	40	60
Jan 02	18.4	7	8	50	0	50	0	0	15	22	64	36

May and August, egg mass was similar (planned contrast; $F = 2.9$, $P = 0.1058$). Residuals from the analysis of covariance on mass of individual eggs were independent of clutch size ($F_{1,28} = 1.4$, $P = 0.2450$), indicating no trade-off between these life history traits (Fig. 6).

DISCUSSION

Fishes exhibit extensive geographic and temporal variation in life history traits (Roff, 1992; Stearns, 1992). Blackbanded Darters are no exception—that is, several life history traits that we quantified in Florida populations differed between the two populations, which are separated by only a few kilometers, as well as across the reproductive season. Some of our findings also differ from those of previous studies conducted at other localities in the Blackbanded Darter's

range (McLane, 1955; Suttkus and Ramsey, 1967; Mathur, 1973).

Reproductive seasonality is variable among fish populations and generally corresponds to geographic variation in environmental conditions such as photoperiod and water temperature (Conover, 1992). Florida populations of Blackbanded Darters initiated reproduction earlier (December–January) than more northerly populations in Louisiana (mid-February; Suttkus and Ramsey, 1967) and Alabama (early May; Mathur, 1973). Earlier initiation of the reproductive season in Florida is not unexpected because darters tend to have longer reproductive seasons in lower latitudes where they are able to initiate spawning activity earlier (Hubbs, 1985). We also found that Florida populations of Blackbanded Darters terminated reproductive activity later in the season (August–September) than populations in
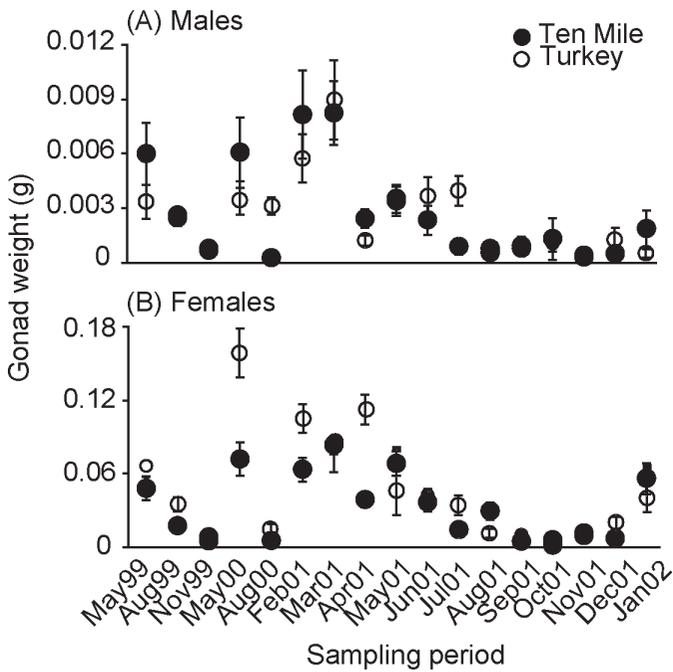
Fig. 3. Seasonal variation in mean (± 1 SE) gonad weight of (A) male and (B) female Blackbanded Darters collected from Ten Mile Creek (closed circles) and Turkey Creek (open circles) in northwestern Florida. Only data for fish larger than the minimum size of reproductive maturity are included (*n* = 990 individuals).

River drainage of Florida may spawn throughout much of the year (McLane, 1955).

Differences in stream thermal regime likely contribute to differences in the duration of reproductive seasons among populations of Blackbanded Darters. Darters living in stenothermal streams tend to have longer reproductive seasons than darters living in eurythermal streams (Hubbs, 1985). Ten Mile and Turkey creeks receive most of their base flow from a sand-gravel aquifer and are therefore thermally more stable compared to previous study locations: Halawakee Creek in Alabama (Mathur, 1973) and the Pearl River in Louisiana (Suttkus and Ramsey, 1967). Blackbanded Darters have a longer reproductive season in Turkey Creek, which is the more thermally stable of our two study populations. In addition to thermal regime, environmental factors such as photoperiod, stream discharge, and availability of food resources also likely contribute to geographic variation in reproductive seasonality of Blackbanded Darters (Schenck and Whiteside, 1977; Marsh, 1980).

Reproductive investment varies seasonally in many darters. Female condition, clutch size, or egg size may increase or decrease throughout the season (James and Taber, 1986; Heins et al., 2004; Khudamrongsawat et al., 2005; Barron and Albin, 2006) or peak mid-season (Marsh, 1984; Hubbs et al., 1968; Barron and Albin, 2006). In Blackbanded Darters in Florida, egg size remained relatively consistent throughout the season. Females invested significantly more energy in the number of offspring produced in the spring than in the late summer. Differences in reproductive investment across these months may have been due to greater availability of food resources at the beginning of the season as well as because females were in better condition. In early spring, females of similar length weighed significantly more than during late summer.

Seasonal variation in clutch size, but not egg size, suggests that female Blackbanded Darters increase reproductive output by producing more eggs rather than by producing larger eggs. Given that Blackbanded Darters do not provide parental care after egg deposition (Page, 1983), investing in a
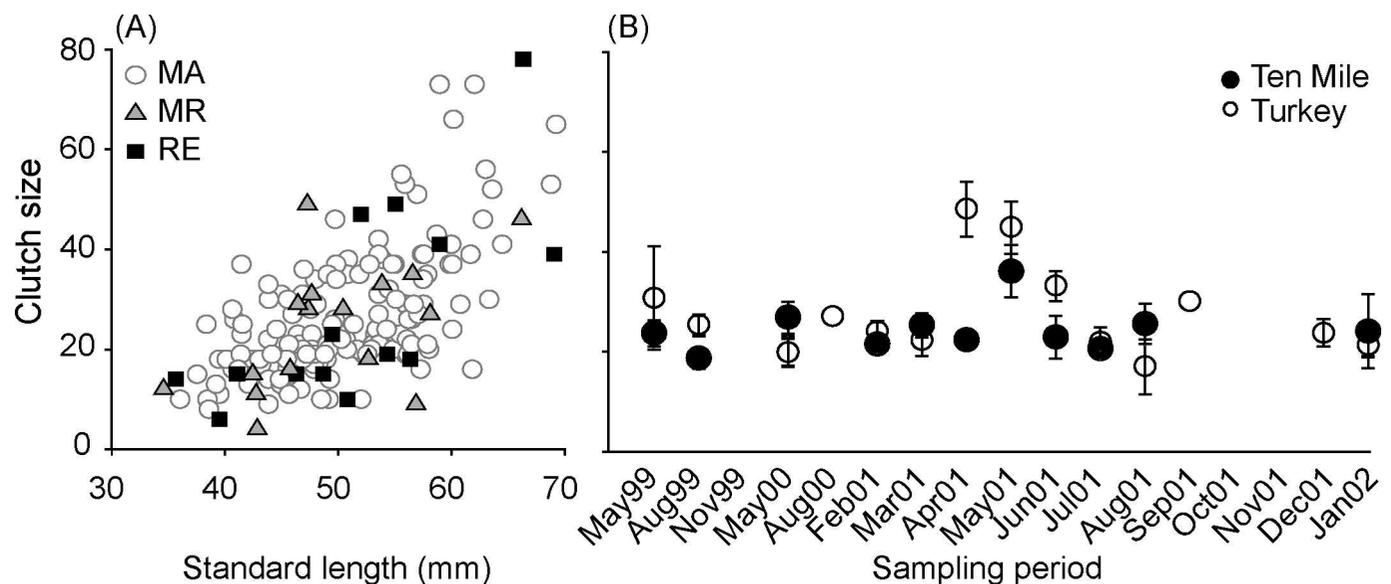
Louisiana (April; Suttkus and Ramsey, 1967) and Alabama (June; Mathur, 1973). This result was unexpected because darter populations in southern latitudes tend to complete annual reproductive activity in the spring (Page, 1983) and cessation of the darter reproductive season does not vary significantly with latitude (Hubbs, 1985). Although reproductively mature Blackbanded Darters were found during most months, there was clearly a decline in the level of activity between our spring and late summer sampling periods. In contrast, Blackbanded Darters in the St. Johns

Fig. 4. (A) Relationship between standard length and clutch size in female Blackbanded Darters. Symbols indicate female maturation stage: mature (MA: open gray circle), mature-ripening (MR: filled gray triangle), and ripe (RE: black squares). We show all three maturation stages although only clutches from mature and mature-ripening females were included in analyses of clutch size. (B) Seasonal variation in mean (± 1 SE) clutch size of Blackbanded Darters collected from two creeks (Ten Mile Creek: closed circles, Turkey Creek: open circles) in northwestern Florida.
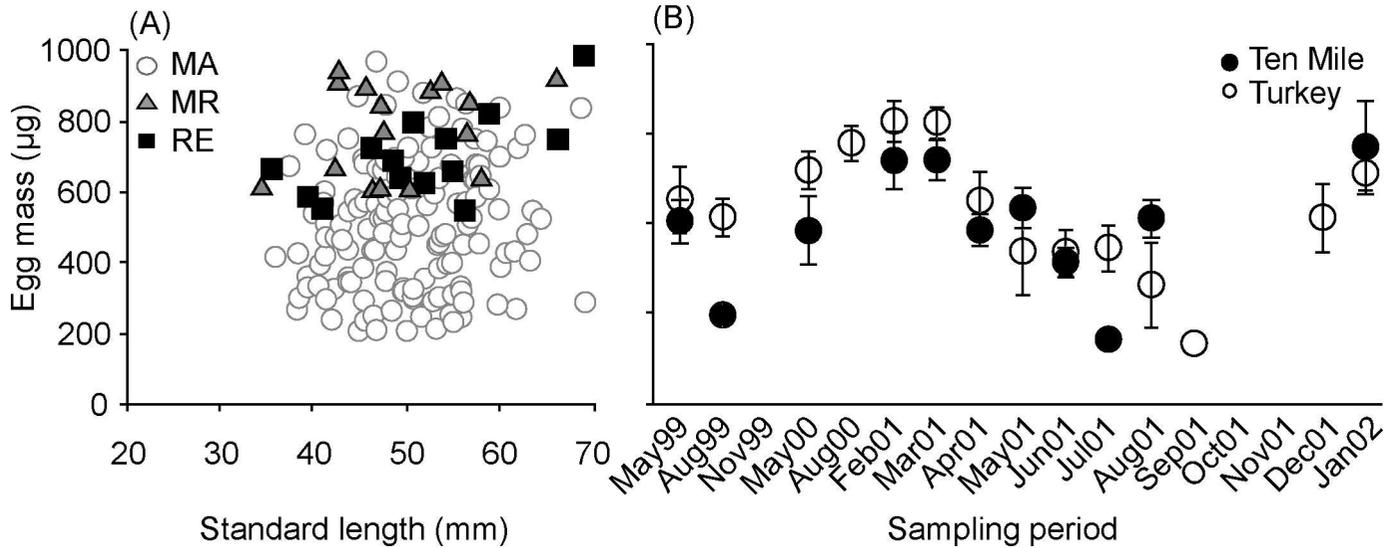
Fig. 5. (A) Relationship between standard length and egg mass in female Blackbanded Darters. Symbols indicate female maturation stage: mature (MA: open gray circle), mature-ripening (MR: filled gray triangle), and ripe (RE: black squares). We show all three maturation stages although only clutches from mature-ripening and ripe females were included in analyses. (B) Seasonal variation in mean ($\pm$ 1 SE) egg mass of Blackbanded Darters collected from two creeks (Ten Mile Creek: closed circles, Turkey Creek: open circles) in northwestern Florida.

larger number of smaller offspring may be the optimal reproductive strategy (e.g., Gross and Sargent, 1985). Alternatively, egg size may be more constrained than clutch size in Blackbanded Darters, as occurs in other darters (Guill and Heins, 1996, 2000) as well as in other fishes (Roff, 1992). The heaviest egg was about twice the mass of the lightest egg, whereas the largest clutch was about 20 times the size of the smallest clutch.

Clutch sizes of Blackbanded Darters in Florida are among the smallest reported for darters in the genus *Percina* (Page, 1983; Kuehne and Barbour, 1984). Clutch sizes in our Florida populations ranged from 4 to 73 eggs, whereas Blackbanded Darters in Alabama had clutch sizes ranging from 38 to 250 eggs (Mathur, 1973). Substantial geographic variation in clutch size is possible, but it is equally likely that methodological differences in categorizing and counting mature eggs explains the difference in clutch sizes between these populations (Heins et al., 1992).

Populations of Blackbanded Darters in Alabama included significantly more males than females, and sex ratio was increasingly biased toward males with increasing size. Mathur (1973) expressed some concern that the male-biased sex ratio he observed in Alabama could in part reflect incomplete sampling of all habitats. This seems unlikely because 1) we found the same male-biased sex ratio in Florida populations and 2) we used a visual collection method that allowed us to sample all size classes of Blackbanded Darters in all habitats (Jordan et al., 2008). Rather than being a sampling artifact, it seems more likely that the decrease in relative abundance of females in larger size classes reflects differential survival of males and females or indicates that females are investing more into reproduction than somatic growth once they reach sexual maturity (Page, 1983; Roff, 1992; Stearns, 1992). Evidence that males are more abundant, grow faster, reach greater maximum size, and/or live longer than females exists for several other species of darters (Raney and Lachner, 1939; Lachner et al., 1950; Karr, 1964; Page and Smith, 1970, 1971; Scott and Crossman, 1973), although there are exceptions (Winn, 1958; Karr, 1963). Sex-specific fitness costs have been studied in a wide variety of vertebrates and invertebrates (Roff, 1992; Stearns, 1992), yet our understanding of the mechanisms underlying differences in life history traits between sexes in darters remains limited.

Spatial and temporal variation in the life histories of Blackbanded Darters likely reflects differences in environmental conditions (e.g., stream thermal regime) between creeks and localities. Additionally, genetic divergence among populations across Louisiana, Alabama, and Florida may contribute to this variation (Malorie Hayes, pers. comm.), a finding that would be consistent with research on other species across the Gulf Coastal Plain (reviewed by Wiley and Mayden, 1985). However, Ten Mile Creek is a
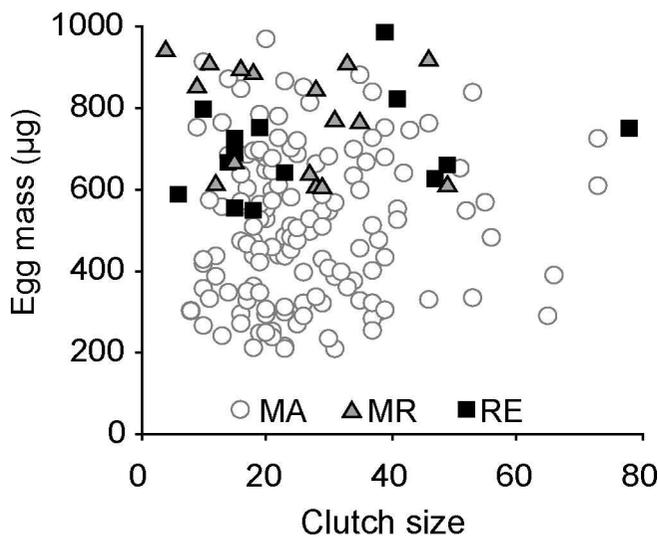

Fig. 6. Relationship between clutch size and egg mass in female Blackbanded Darters collected from two creeks in northwestern Florida. Symbols indicate female maturation stage: mature (MA: open gray circle), mature-ripening (MR: filled gray triangle), and ripe (RE: black squares).

tributary of Turkey Creek, so it seems unlikely that the populations we studied in Florida are significantly genetically divergent from one another (Austin et al., 2011).

Rigorously testing hypotheses about the mechanisms underlying observed spatial and temporal variation in life history traits of Blackbanded Darters was beyond the scope of this study. Nonetheless, our findings add to a growing body of research that emphasizes the importance of assessing information from several localities and at several points in time to determine if variation in life history traits exists. Moreover, documentation of spatial and temporal variation in life history traits helps identify species that would be ideal candidates for comparative and experimental research on patterns and causes of life history variation.

ACKNOWLEDGMENTS

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