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Predator Environment Does Not Predict Life History in the Morphologically Constrained Fish *Alfaro cultratus* (Cyprinodontiformes: Poeciliidae)

***Kaitlyn B. Golden*[1]*, *Mark C. Belk*[1] and *Jerald B. Johnson*[1,2]**

[1] Department of Biology, Evolutionary Ecology Laboratories, Brigham Young University, Provo, UT, United States, [2] Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT, United States

Edited by:
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Germany

****Correspondence:***
Kaitlyn B. Golden
kaitlynbgolden@gmail.com

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Predation is known to have a significant effect on life history diversification in a variety of species. However, physical constraints of body shape and size can sometimes limit life history divergence. We test this idea in the Costa Rican livebearing fish *Alfaro cultratus*. Individuals in this species have a narrow body and keeled ventral surface, and females do not develop a distended abdomen when pregnant like other livebearing fishes. Here, we describe the life history of *A. cultratus* from 20 different populations across both high-predation and low-predation environments. We found significantly lower reproductive allotment in females from high-predation environments than in females from low-predation environments, but no significant difference in female or male size at maturity, number of offspring produced by females, or size of offspring. We found that *A. cultratus* exhibit isometric patterns of allocation for clutch dry mass in relation to female dry mass in high-predation and low-predation environments. Our results suggest that body shape constraints in this species limit the life history divergence we typically see between populations from high-predation and low-predation environments in other species.

Keywords: Poeciliidae, life history, *Alfaro cultratus*, allometry, constraints, predation, terminal investment hypothesis

INTRODUCTION

A life history strategy defines how an organism utilizes and optimizes energy to survive and reproduce (Fisher, 1930; Williams, 1966; Stearns, 1977; Roff, 1992). The optimal strategy can be influenced by extrinsic factors such as mortality rate (Strauss, 1990; Jennions et al., 2006; Riesch et al., 2013; Mukherjee et al., 2014; Olinger et al., 2016), resource availability (Reznick et al., 1992; Riesch et al., 2013; Moore et al., 2016; Zandonà et al., 2017), population density (Bronikowski et al., 2002; Schrader and Travis, 2012), and environmental conditions (e.g., salinity, gradient, elevation, etc.) (Zúñiga-Vega et al., 2007; Jourdan et al., 2016; Rius et al., 2019). Predator environments have often been used to study the effects of mortality rate on life history strategies (Law, 1979; Reznick and Endler, 1982; Johnson and Belk, 1999; Gosline and Rodd, 2008) and have been found to affect a wide variety of taxa, including fish, anurans, and insects. Among other things, the presence of a predator can influence timing and size of maturation and changes among developmental stages (Chivers et al., 2001; Johnson, 2001; Hilton et al., 2002; Stoks et al., 2006; Peterson et al., 2019), growth rate (Lardner, 2000; Altwegg, 2002; Šupina et al., 2016; Brown et al., 2018; DeWitt et al., 2019), and investment in offspring (Johnson and Belk, 2001; Gorini-Pacheco et al., 2017). Previous work consistently finds divergent life history patterns in high-predation and low-predation environments. For example, in the family Poeciliidae (livebearing fishes) many studies have shown a divergent pattern of smaller size at maturity, higher fecundity, smaller offspring, and greater reproductive allotment in populations in high-predation environments relative to low-predation or no-predator environments (Reznick, 1990; Johnson, 2001; Jennions and Telford, 2002; Walsh and Reznick, 2009; Moore et al., 2016). Similarly, in anurans the timing and size of metamorphosis (Laurila et al., 1998; Lardner, 2000) and timing of hatching (Laurila et al., 2002; Capellán and Nicieza, 2007) change in response to the presence of a predator. Therefore, we expect to see patterns of life history divergence in response to predator environments in additional species.

There are limits, however, to divergent evolution in predator environments. Divergent evolution requires that populations are able to adapt to different selective pressures. That said, there are genetic, phylogenetic, morphological, and physiological constraints that can all limit adaptive evolution (Gould, 1980). Morphological constraints are particularly important in life history evolution as they can affect the internal body space available for reproduction. This has been frequently studied in turtles (Clark et al., 2001; Ryan and Lindeman, 2007; Rollinson and Brooks, 2008; Macip-Ríos et al., 2012). For example, the small African tortoise *Homopus signatus*, produces single-egg clutches. Although producing one large egg is best for the fitness and survival of the offspring, *H. signatus* is constrained by a small body size and pelvic canal limiting how large the egg can be (Hofmeyr et al., 2005). Similar patterns were found in other species of turtles where the pelvic girdle (also influenced by evolutionary pressures on locomotion) limited egg size, especially in small individuals (Congdon and Gibbons, 1987). Thus, morphology can constrain a life history trait due to internal space, size, and shape of an organism.

Morphology is also important in survival; tradeoffs between the optimal morphology for survival and the optimal morphology for reproduction may be present in some species. Size and shape can be very important in predator avoidance. For example, the humpback chub, *Gila cypha*, has a large dorsal cranial hump that increases the depth of their body and therefore protects against gape limited predators (Portz and Tyus, 2004). Tradeoffs occur because certain morphologies may be optimal to some selective pressures, but not to others. In the family Poeciliidae, fishes invest more in offspring when predators are present than when they are absent; however, this investment comes at a cost of decreased swimming performance (Ghalambor et al., 2004). Thus the optimal morphology for swimming performance and the optimal morphology for reproduction can be in conflict (Zúñiga-Vega et al., 2007; Wesner et al., 2011; Hassell et al., 2012; Ingley et al., 2016; Quicazan-Rubio et al., 2019). Selective pressures acting on morphology can limit the optimal adaptation in life history or vice versa in a given environment. However, we don't know how morphological adaptations limit life history adaptations in predation environments.

An additional question is how predation and morphological constraints influence lifetime reproductive allocation. The terminal investment hypothesis predicts that organisms will invest more in reproduction as they age, as chances for future reproduction decrease (Williams, 1966). Specifically, in environments that experience high mortality (such as high-predation environments) individuals may allocate energy to current reproduction over future reproduction; however, in low mortality environments (such as low-predation environments) individuals may allocate more to future reproduction than current reproduction, consistent with the terminal investment hypothesis (Law, 1979; Michod, 1979; Billing et al., 2007; Belk et al., 2011; Billman et al., 2014; Nickley et al., 2016). Thus, reproductive allocation can change in response to mortality pressures presented in predation environments as high mortality limits the chance of survival and opportunities for future reproduction. Morphological constraints can also influence within-lifetime reproductive allocation. In *Brachyrhaphis parismina* (a poeciliid fish), populations showed isometric allocation of reproductive allotment to female body mass with age (Belk et al., 2011). This is possibly due to a narrow-bodied shape that might constrain reproductive allocation from being greater than proportionate to body size. Thus, mortality rates and morphological constraints can influence patterns of reproductive investment.

In this study, we test the ideas that: 1) divergence in life history traits among populations in different predator environments may be limited when there are strong morphological constraints; and 2) within lifetime reproductive allocation, consistent with the terminal investment hypothesis, may be limited within predation environments due to morphological constraints. If true, we expect to find isometric allocation rather than hyper-allometric allocation in morphologically constrained species. To test these ideas, we used the fish *Alfaro cultratus* (Regan, 1908) from the family Poeciliidae. Poeciliids provide an optimal study system as they are livebearers, have a short generation time, and are found in many different selective environments (Reznick and Endler, 1982). *Alfaro cultratus* is an ideal species for our study as it is an extremely narrow-bodied poeciliid with a keeled ventral surface (**Figure 1**). Additionally, *A. cultratus* do not develop a distended abdomen during pregnancy. The body morphology of this fish is likely a constraint for reproduction as it does not allow additional space via abdominal expansion during pregnancy as exemplified in other poeciliids.

MATERIALS AND METHODS

Study Sites, Collections, and Characterizing Predation Environments

We collected fish from eight different sites in Costa Rica during February and May 2006, and May 2007. Additionally, we collected *A. cultratus* from 12 different sites in northeast

FIGURE 1 | Photos of the lateral and dorsal view of a female *Alfaro cultratus*. Dorsal view shows laterally compressed body shape.

Costa Rica during April 2019 (**Figure 2**). We collected fish under Brigham Young University IACUC committee approval (Protocol #15-0404). All fish were collected with permission and corresponding permits from the Sistema Nacional De Áreas De Conservación in Costa Rica (011-2006-SINAC, 015-2007-SINAC, R-SINAC-PNI-ACAHN-011-2019). We collected samples with a handheld seine (1.3 × 5 m; 8 mm mesh size). We tried to collect approximately 100 females (**Table 1**) from each site to ensure that we had enough mature and immature individuals for analysis without taking more than a fraction of the local population. We euthanized all fish in the field with an overdose of 3- amenobenzoic acid ethyl ester (MS-222), preserved samples in the field in 95% ethanol, and then transported them to the laboratory for analysis where they were stored in 70% ethanol.

We identified high-predation sites as locations where the piscivorous species *Parachromis dovii* (Johnson and Belk, 2001) and/or *Parachromis managuensis* were found during seining. At each location we made multiple seine hauls (10 or more). Low-predation sites were identified as locations where *A. cultratus* was found alone or only with non-piscivorous fishes. Here, we analyze 11 high-predation sites (one from 2006, three from 2007, and seven from 2019) and nine low-predation sites (two from 2006, two from 2007, and five from 2019). We term these sites as "high predation environments" or "low-predation environments," respectively. High-predation and low-predation environments are expected to vary in predation risk but also may be confounded with other environmental factors such as resource availability, temperature, elevation, flow, and density (Johnson, 2002; Jourdan et al., 2016; Olinger et al., 2016). Thus, predation environments are characterized by the presence or absence of a predator, but they are called "environments" to encompass the many different factors that may be causally or incidentally correlated with the presence or absence of a predator (see Johnson, 2002). In addition to piscivorous predators, other factors can contribute to morality rates, including avian and invertebrate predators. Previous work on the fish *Brachyrhaphis rhabdophora* suggests that categorizing locations this way into high and low-predation environments does accurately predict mortality rates and divergent life history traits (Johnson and Belk, 2001; Johnson, 2002; Johnson and Zúñiga-Vega, 2009). Therefore, although we have not measured mortality rates in this system, we use the presence/absence of a predator as a predictor of mortality (Johnson, 2001; Johnson and Belk, 2001; Belk et al., 2011; Wesner et al., 2011).

Life History

We measured five life history traits: 1) male size at maturity; 2) female size at maturity; 3) number of offspring; 4) size of offspring; and 5) reproductive allotment. All traits were measured from alcohol-preserved specimens. We recognize that this preservation technique results in the extraction of fats from

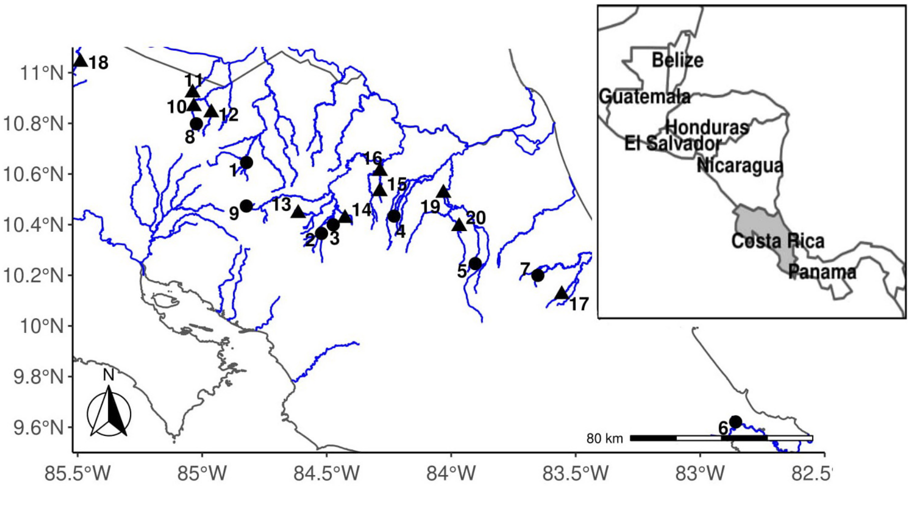

FIGURE 2 | Map of Costa Rica collection locations. Localities are numbered according to the site number found in **Table 1**. High-predation sites are triangles; low-predation sites are circles.

TABLE 1 | Descriptive statistics for life history characteristics of *Alfaro cultratus* for 20 populations.

	Location	Year	Site Number	Number of Males	Mean length of adult males (mm)	Size range of adult males (min–max)	Number of Females	Minimum size of gravid females (mm)	Brood Dry Mass (mg)	Number of Offspring	Offspring Size (mg)	Mean Female Dry Mass (mg)
Low-predation Sites	Rio Queque	2019	1	6	34.14	30–42.8	33/54	32	0.009	9.714	0.00101	0.115
	Rio Balsa Tributary	2019	2	40	34.4	28.1–41.7	56/156	34	0.008	7.491	0.00114	0.142
	Quebrada Serena	2019	3	48	33.33	28.2–43	65/94	34	0.019	18.145	0.00110	0.136
	Quebrada Sahino	2019	4	14	33.86	30–42	49/90	32	0.009	6.200	0.00159	0.078
	Rio Sucio	2019	5	13	34.78	28.2–42.6	32/50	34	0.011	13.397	0.00083	0.098
	Trib. To Rio Sixaola	2007	6	14	26.486	21.7–38.1	24/33	30	0.008	7.431	0.00123	0.099
	Trib. to Rio Parismina	2007	7	11	36.291	28.9–41.5	20/21	30	0.009	7.765	0.00124	0.247
	Rio Salto	2006	8	21	31.433	25.3–52.7	27/82	28	0.012	11.862	0.00151	0.100
	Quebrada Perez	2006	9	7	39.643	30–46.5	12/57	42	0.022	27.744	0.00069	0.184
High-predation Sites	Rio Zapote (Side Channel)	2019	10	18	33.35	25.9–47.6	32/96	34	0.019	17.888	0.00107	0.128
	Quebrada Las Latas	2019	11	57	30.34	23–43.2	59/108	28	0.009	9.001	0.00108	0.131
	Rio Ricardo	2019	12	22	37.65	31.9–43.8	43/76	34	0.011	10.840	0.00106	0.125
	Quebrada Piedra	2019	13	20	35.28	23.9–44.6	60/106	34	0.011	10.243	0.00113	0.115
	Rio San Rafael Tributary	2019	14	35	32.37	26.8–41.4	55/114	30	0.008	6.395	0.00127	0.130
	Quebrada Huevo	2019	15	26	33.37	27.7–41.5	46/130	32	0.013	9.412	0.00147	0.124
	Rio Saino	2019	16	24	30.58	25.5–38.3	43/98	34	0.014	12.121	0.00119	0.097
	Rio Herediana	2007	17	13	40.523	35.5–46.8	27/104	40	0.012	13.657	0.00092	0.220
	Rio Sabalo	2007	18	17	35.465	25.7–47.3	17/90	42	0.006	6.921	0.00086	0.244
	Trib. to Rio Sarapiqui	2007	19	21	34.814	26.4–45.8	49/92	32	0.010	10.993	0.00100	0.179
	Isla Grande	2006	20	13	30.339	25.3–41.6	19/73	32	0.004	9.254	0.00086	0.096

Brood size, number of offspring, and size of offspring are least squares means that come from the linear models reported in the text. Brood size and number of offspring least squares means have been back transformed to represent true numeric values. Number of females for populations in 2006 and 2007 are reported only as the number that were mature out of the number dissected; for 2019 populations these include all females collected.

the specimens, an approach that has been applied widely across life history studies, including in our previous work (Johnson and Belk, 2001; Belk et al., 2011; Brown et al., 2018; Molina-Moctezuma et al., 2020), thus allowing us to compare findings here with previous work. We collected life history data using methods described in Johnson and Belk (2001). In brief, we did this as follows. We first measured the length of each adult female fish. We then dissected each specimen on the left lateral side where we removed stomachs and embryos. We counted and staged each embryo. To score female size at maturity for each population, we first divided females into 2 mm size classes. We identified size at maturity as the size class where at least half of the females were mature with developing embryos. Developing embryos were classified using Haynes (1995) classification method (stages 1–11). Stage 1 and 2 are immature and unfertilized eggs, and stage 3 and above are developing embryos. Stage 3 is a fully yolked and fertilized egg, and stage 11 is a mature embryo with the yolk sac entirely, or almost entirely, absorbed (Haynes, 1995). In cases where population samples of mature females were small, the actual value may be slightly smaller or larger than reported because we lacked adequate sampling. We counted number of offspring as the number of developing embryos contained in each mature female. We determined size of offspring as the dry mass of the brood divided by the number of offspring in each brood. We measured reproductive allotment as the dry mass of the brood. Female dry mass (digestive tract removed) and brood dry mass were measured after they were separated and dried for 24 h in a 55°C desiccating oven. We determined male size at maturity as the mean standard length of all mature males (male poeciliids grow little, if at all, after maturation) (Turner, 1942; Johnson and Belk, 2001; Belk et al., 2011). We identified mature males by the presence of a fully developed modified anal fin (gonopodium).

Allometry Analysis

We built two models of reproductive allotment as the relationship between the natural log of clutch dry mass and the natural log of female dry mass in both high-predation and low-predation environments. We used the slopes of these models as allometric coefficients (**Table 2**). We included developmental stage of offspring as a covariate and collection location as a random effect in the models. We determined patterns of allometry using ordinary least squares regression (Kilmer and Rodríguez, 2017). When the slope was equal to one, this indicated isometry and not terminal investment. A slope greater than one is consistent with terminal investment (Billman et al., 2014), where the mass of the clutch is proportionately larger than predicted by body size. Females exhibit indeterminate growth; thus, we used size of females as a surrogate of age. All analyses were done using R version 3.5.2 (R Project for Statistical Computing, RRID:SCR_001905).

Life History Trait Analysis

We ran general linear models for each life history trait to assess the effect of predation. We included covariates for the life history models as described in Johnson and Belk (2001). In brief, when analyzing number of offspring, we included female dry mass as a covariate. When analyzing offspring size and reproductive allotment, we used female dry mass and developmental stage of embryos as covariates. We did not include any covariates for male or female size at maturity. Brood dry mass was our measure of reproductive allotment. We log transformed reproductive allotment and number of offspring in the analysis to satisfy assumptions of the linear model. All output data for reproductive allotment and number of offspring were back-transformed to the original scale before being included in graphs or tables. We included location in each model as a random effect. We calculated population least squares means for reproductive allotment, number of offspring, and size of offspring for comparable estimates (**Table 1**). Additionally, we ran the analysis for reproductive allotment with and without the population from Quebrada Serena (a possible outlier) to determine the significance of this population. We found that with the removal of this site, predation no longer significantly affected reproductive allotment. All analyses were done using R version 3.5.2 (R Project for Statistical Computing, RRID:SCR_001905).

TABLE 2 | Allometric coefficients for *Alfaro cultratus* in high-predation and low-predation environments.

Predator	Allometric Coefficient (AC)	SE	95% CI	AC > 1	Intercept
High	1.052	0.061	0.932–1.172	No	−3.161
Low	1.083	0.081	0.924–1.243	No	−2.753

Isometry is seen in high-predation and low-predation environments as evidenced by confidence intervals that span a slope of 1.

RESULTS

Life history traits in *A. cultratus* did not differ significantly between high-predation versus low-predation environments except reproductive allotment (**Table 3**). Females from high-predation environments had significantly lower values of reproductive allotment than those from low-predation environments (ANCOVA, $F = 5.7$, $df = 1$, $P = 0.017$, slope = −0.15, $R^2 = 0.46$). The statistical significance of this relationship is entirely due to one population with high

TABLE 3 | Statistical tests for effect of predation environments on the five life history traits.

Life History Trait	*F*	*df*	*P*-value	Slope	R^2	Intercept
Reproductive Allotment	5.730	1	0.017	−0.1500	0.455	−5.702
Number of Offspring	1.118	1	0.291	−0.0700	0.401	1.659
Offspring Size	2.975	1	0.085	−0.0001	0.089	0.001
Female Size at Maturity	1.011	1	0.315	0.3170	0.002	32.284
Mean Male Size at Maturity	1.266	1	0.261	0.2860	0.003	33.308

Female dry mass and development stage are covariates for reproductive allotment and offspring size. Development stage is a covariate for number of offspring. Location is included as a random effect in each model.

brood dry mass in the low-predation category (Quebrada Serena) (see S1, **Supplementary Material**). Size of offspring, number of offspring, and size at maturity for males and females did not differ significantly in high-predation versus low-predation environments (**Table 3** and **Figures 3**, **4**).

Similarly, the allometric coefficients for reproductive allotment did not differ between high-predation and low-predation environments. Individuals in both environments displayed isometric reproductive allocation with age, inconsistent with the terminal investment hypothesis (**Table 2** and **Figure 5**).

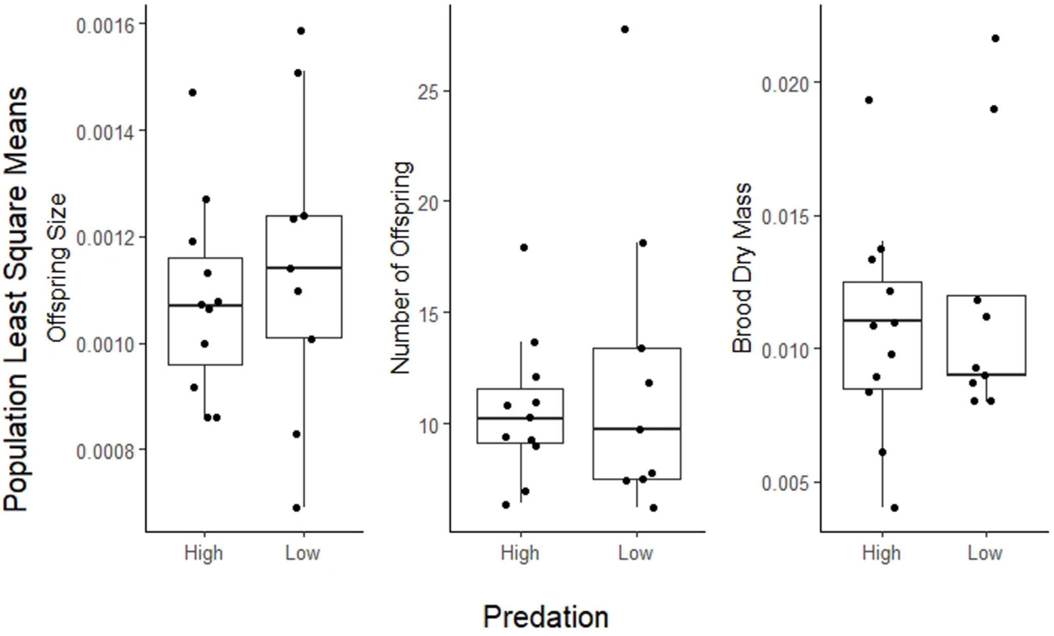

FIGURE 3 | Plot of population least squares means for reproductive allotment (brood dry mass), number of offspring, and size of offspring in high-predation and low-predation environments. Population means (dots) are jittered for better visualization.

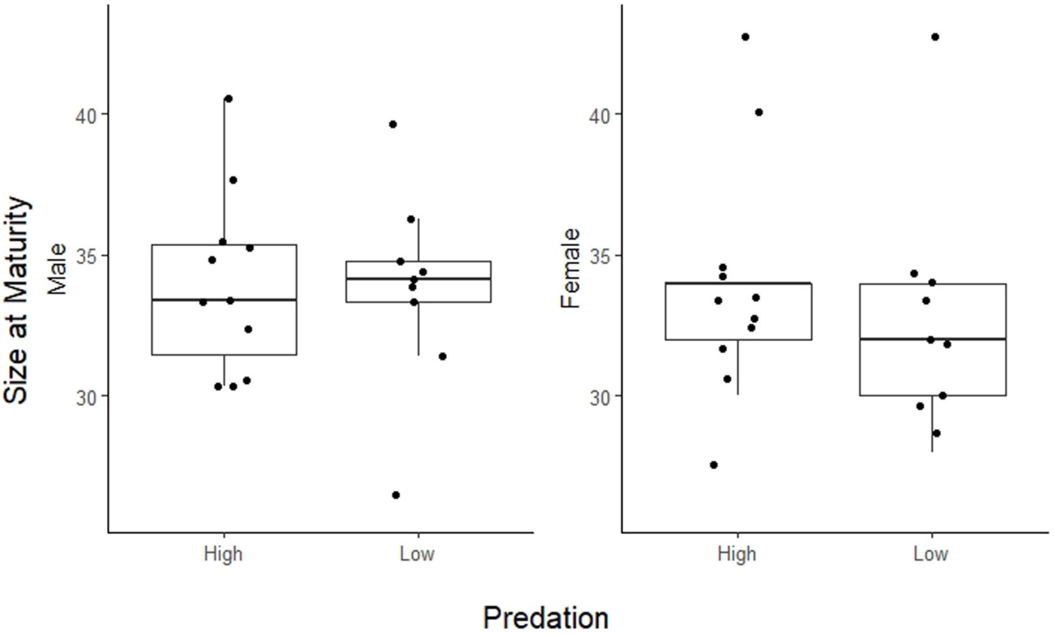

FIGURE 4 | Plot of size at maturity for males and females in high-predation and low-predation environments. Female size at maturity is the size where at least 1/2 females in that size category contain developing embryos. For males this is the mean size of mature males. Population points (dots) are jittered for better visualization.

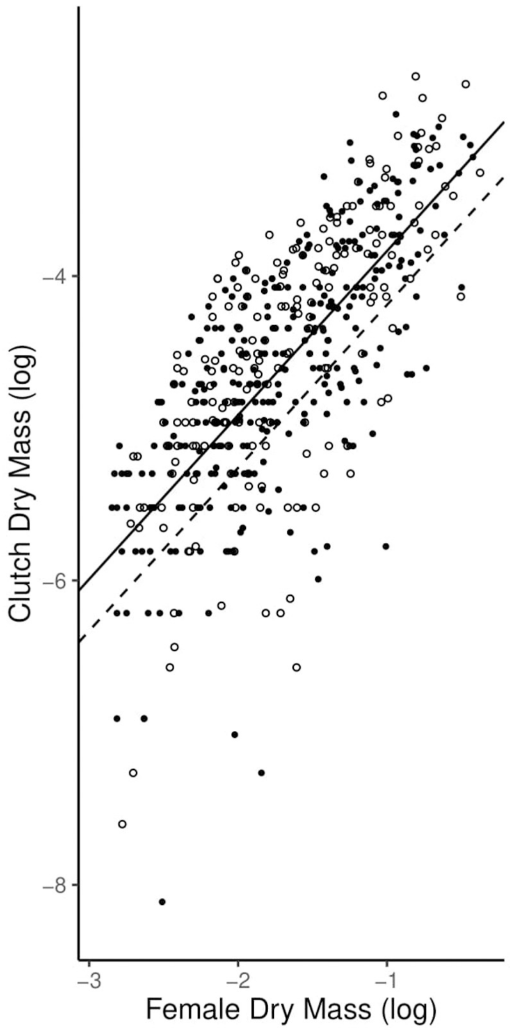

FIGURE 5 | Graph of allometric coefficients for high-predation and low-predation environments. Low-predation sites are open circles and high-predation sites are closed circles. The low-predation allometric coefficient (1.052) is the dashed line and the high-predation allometric coefficient (1.083) is the solid line.

DISCUSSION

There was no divergence in four life history traits or allometric coefficients for reproductive allotment in *A. cultratus* from different predation environments. All life history traits showed no significant difference between high-predation and low-predation environments, except for reproductive allotment, which did differ significantly. However, it differed in a direction opposite to what theory predicts (Reznick, 1990) – we found lower allotment in high-predation environments than in low-predation environments. This significant result and allotment pattern are driven by our collection from Quebrada Serena (site 3). With the removal of this site, the difference in reproductive allotment is no longer significant. This site appears to be unique in that all mature females had a large number of offspring (greater than 8). However, it does not appear to be unique in any other way. Thus, it is possible that the life history phenotype observed at this site is shaped by other selective pressures. One possible explanation is resource availability. High resource availability has been found to influence a high fecundity (Reznick and Yang, 1993) and with the high fecundity found at this site this may be a likely explanation. The allometric coefficient for reproductive allotment also did not differ among predation environments but instead showed an isometric pattern of allocation in both environments. This isometric pattern of investment is not consistent with the terminal investment hypothesis. Thus terminal investment is not evident in this species.

Lack of intraspecific life history variation is not unique to *Alfaro cultratus.* Absence of significant life history differences between populations is also seen in the species *Brachyrhaphis parismina* (Belk et al., 2011). However, differing predation pressures often evoke a divergent pattern of life history variation as is seen in *Brachyrhaphis rhabdophora*, *Brachyrhaphis episcopi*, and *Poecilia reticulata* (Reznick and Endler, 1982; Johnson and Belk, 2001; Jennions and Telford, 2002). The almost complete lack of intraspecific life history divergence across predation environments in *Alfaro cultratus* is unexpected and requires further exploration.

There are several possible explanations for the lack of divergence in life history in *A. cultratus*. It is possible that there may not be differences in environmental selective pressures among the sites. In environments where multiple factors are highly correlated, using one factor such as predator presence, is sufficient in representing a suite of putative selective agents at sites (Johnson, 2002). If environmental factors are not highly correlated, then using one factor such as predation may not adequately represent variation among selective environments. It is also possible that our predation environment as categorized here does not accurately predict mortality rates. Variation in actual mortality rates among localities could prove problematic to our simple placement of populations into either high or low mortality groups. This said, such categories have proved effective at predicting mortality rates in other systems (Johnson and Belk, 2001; Johnson and Zúñiga-Vega, 2009; Ingley et al., 2014; Belk et al., 2020). Lack of phenotypic divergence might also be attributed to gene flow between populations that can limit the ability of populations to adapt to selective pressures in their environment and therefore decrease differences between populations (Storfer, 1999). Unfortunately, we currently have no estimates of gene flow for this species – this said, the geographic distribution of high-predation and low-predation populations suggest that this explanation is not likely (**Figure 2**). Another alternative is that there is limited additive genetic variation. Again, we have no direct measure of additive genetic variation for *A. cultratus*. None of these explanations were examined in full in this study, but they may be a good direction for future research.

The most obvious explanation for lack of variation in this narrow-bodied species is that morphology acts as a constraint on reproductive traits. Body morphology influences swimming performance and predator avoidance (McPeek et al., 1996; Kolar and Wahl, 1998; Langerhans et al., 2004; Langerhans, 2009; Araújo et al., 2017). Pregnancy, in many species of poeciliids, can drastically change swimming performance causing predator avoidance to decline as pregnancy progresses (Ghalambor et al., 2004; Belk and Tuckfield, 2010). This may be caused by a morphological convergence across species during pregnancy which limits burst swimming near the end of pregnancy as the abdomen becomes distended and reproductive investment is favored over predator escape speed (Ghalambor et al., 2003; Wesner et al., 2011; Ingley et al., 2014). Some species are able to moderate the distension of the abdomen during pregnancy by superfetation, the simultaneous carrying of multiple broods, and thus maintain a more streamlined body morphology during pregnancy (Zúñiga-Vega et al., 2007; Fleuren et al., 2019). *Alfaro cultratus* does not exhibit superfetation, instead, their narrow body appears to limit abdominal distension during pregnancy. We suggest that the narrow body and distinctive ventral keel are important for swimming ability and that swimming ability may be favored in all environments in this species. Thus, limiting the space available at the end of pregnancy for a distended abdomen and contributing to the lack of difference seen among populations and individuals in life history characteristics.

For *Alfaro cultratus*, both the ventral keel and the narrow, streamlined body shape likely contribute to stabilized swimming ability. Morphological adaptations in fish are critical to increasing thrust and decreasing drag despite swimming style (e.g., stead or unsteady) (Webb, 1984). Small differences in morphology can have a large effect on locomotion (Webb, 1982), with body shape and fins both playing important roles in swimming performance (Blake, 2004; Langerhans and Reznick, 2010). First, a keeled ventral surface has been shown to be important in swimming performance (George and Westneat, 2019). In scombroid fishes, the presence of a keel on both sides of a caudal peduncle decreases drag and is more efficient than a cylinder or vertically elliptical peduncle (Walters, 1962). A keeled surface increases the surface area that is used for thrust (Graham and Lowell, 1987). Specifically, a ventral keel creates a negative pressure that increases stabilization and resistance to rolling (Van Wassenbergh et al., 2015). The ventral keeled surface of *Alfaro cultratus* may contribute to swimming performance by increasing stability for steady swimming. Second, a narrow-bodied morphology can likewise be beneficial for steady swimming. The body morphology of a fish influences energy demands by favoring either steady or unsteady swimming (Ohlberger et al., 2006). A streamlined body shape reduces turbulence and energetic costs (Araújo et al., 2017). Thus, the thin, streamlined body shape of *Alfaro cultratus* likely contributes to steady swimming, allowing for cruising at low energy costs (**Figure 1**). Both the ventral keel and the streamlined morphology of *A. cultratus* appear to be adaptations for steady swimming.

Typically, we would not expect to see stabilized swimming or the same morphology in all predation environments. Previous studies have found that in high-predation environments, unsteady swimming is favored but in low-predation environments steady swimming is favored (Langerhans, 2009; Langerhans and Reznick, 2010). Maintaining the same morphology in both high-predation and low-predation environments is thought to be costly as morphological divergence across predator regimes is commonly found in prey fish (Langerhans et al., 2004). The optimal morphology in a high-predation environment must be suboptimal in a low-predation environment or else we would expect to see the same morphology in both (Langerhans et al., 2004). No measure of morphological divergence in predation environments has been assessed in this species. Therefore, divergence may occur across predator regimes despite the persistence of a streamlined morphology. The narrow-bodied morphology may be influenced by other factors such as selective pressures like stream flow and resource acquisition as well as behaviors like habitat preference and foraging habits. For example, little is known about the habitat preference and foraging habits of *A. cultratus*. However, if foraging occurs in high flows, this may influence a steady swimming morphology despite suboptimal escape maneuvers that are limited in direction because of high flows (Anwar et al., 2016). It is important to acknowledge that body shape and life history may be unassociated. Fish with the same body shape may have varying patterns of life history if the gonads of the fish simply displace other internal organs (Zúñiga-Vega et al., 2011). Further work is needed to directly assess body shape, swimming performance, and selective pressures in this species.

In conclusion, divergent evolution in different predation environments was not seen in *Alfaro cultratus*. It appears that the ability for divergent evolution to occur in *A. cultratus* in response to predation pressures may be constrained by a narrow-bodied morphology adapted to stabilized swimming performance. Clearly, additional research focused on the cause of the lack of divergence in life history traits in this species will yield promising results.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study was done on preserved specimens.

AUTHOR CONTRIBUTIONS

All authors formulated the idea for the study and conducted fieldwork. JJ and KG oversaw collection of life history data. KG collected 2019 female life history data, performed the analyses, and wrote the first draft of the manuscript. All authors reviewed and edited the manuscript, and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.607802/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.