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Population-Level Responses of Life History Traits to Flow Regime in Three Common Stream Fish Species

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Population-level responses of life history traits to flow regime in three common stream fish species

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3 1 **Population-level responses of life history traits to flow regime in three common stream fish**
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6 2 **species**
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45 19 **Running head:** Fish intraspecific flow-life history relationships
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47
48 20 **Keywords:** flow-ecology, reproduction, trait-based, functional trait
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ABSTRACT

Trait-based approaches may improve understanding in ecology by linking environmental variation to fitness-related characteristics of species. Most trait-environment studies focus on assemblage-level relationships; yet intraspecific trait variation is important for community, ecosystem, and evolutionary processes and has substantial implications for these approaches. Assessing population-level trait-environment relationships could test the generality of trait models while assessing intraspecific variation. We evaluated the generality of the trilateral life history model (TLHM of Winemiller and Rose 1992: opportunistic, periodic, and equilibrium endpoints) for fishes - a well-studied trait-environment model at the assemblage level - to populations of three stream fishes in the Midwestern United States in relation to flow regime. The TLHM adequately described major trade-offs in traits among populations in all species. Some TLHM flow-based predictions were confirmed, with periodic traits (high fecundity) favored at sites with greater flow seasonality and lower flow variability in two species, and equilibrium traits (large eggs) in more stable flow conditions in two species. Size at maturity was also inversely related to variability in one species. However, relationships contradicting the TLHM were also found. Coupled with the explanatory power of the TLHM for populations, supporting relationships suggest that synthesizing habitat template models with demographic life history theory could be valuable. Trait-environment models that are well-supported at multiple levels of biological organization could improve understanding of the impacts of environmental change on populations and communities and the valuable ecosystem services that they support.

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8 49 **INTRODUCTION**

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10 Trait-based approaches are of increasing interest in community ecology because
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12 combining information on environmental conditions (i.e., environmental filters; Smith and
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14 Powell, 1971; Poff, 1997) with data on species traits that directly influence fitness could generate
15
16 a more general and mechanistic understanding of community assembly (Poff, 1997; McGill *et*
17
18 *al.*, 2006). Such approaches have provided major insights into environmental influences on
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20 community assembly in fresh waters (e.g., Poff and Allan, 1995; McManamay and Frimpong,
21
22 2015) and can serve as useful frameworks for developing flow-ecology hypotheses and
23
24 environmental flow standards (McManamay *et al.*, 2014).
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29 The focus of most trait-environment studies to date has been on assemblage-level
30
31 relationships; yet population-level trait variation also has important implications for these
32
33 approaches. Intraspecific trait variability can influence community assembly, community
34
35 stability, and ecosystem function (Luck *et al.*, 2003; Crutsinger *et al.*, 2006; Ackerly and
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37 Cornwell, 2007; Albert *et al.*, 2010), as well as the fundamental evolutionary processes of
38
39 adaptation and speciation (Darwin, 1861). Therefore, assessment of trait-environment
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41 relationships at the population level could further test the generality of trait-based models while
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43 also estimating intraspecific trait variability (Verberk *et al.*, 2013). Here, we provide a field-
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45 based evaluation of the generality of a trait-environment model that has been well-studied at the
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47 assemblage level in populations of three widespread stream fishes in the Midwestern United
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49 States.
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4 69 The trilateral life history model (TLHM), a trait-environment model developed for fishes
5
6 70 by Winemiller and Rose (1992), reflects trade-offs between juvenile survival, fecundity, and
7
8 71 generation time. The endpoints of the TLHM represent life history strategies that are selected for
9
10 72 under certain environmental conditions (Figure 1). The opportunistic strategy minimizes
11
12 73 generation time, which promotes rapid population growth and should be favored in highly
13
14 74 variable environments. The equilibrium strategy maximizes juvenile survival through large eggs
15
16 75 or parental care and should be favored under stable environmental conditions that promote
17
18 76 investment in few, well-provisioned offspring. The periodic strategy maximizes fecundity by
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20 77 delaying reproduction until a larger size is reached and is favored under predictably variable or
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22 78 highly seasonal environments where reproduction can coincide with favorable conditions.
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27 79 Studies from across the globe have largely confirmed fish life history trait ordination along these
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29 80 three axes (e.g., Vila-Gispert *et al.*, 2002; [Olden and Kennard, 2010](#)) and have documented the
30
31 81 utility of the TLHM for predicting assemblage-level life history traits in relation to natural and
32
33 82 altered flow regimes (e.g., [Olden and Kennard, 2010](#); [Mims and Olden, 2012, 2013](#)).

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36 83 Although applied at the assemblage level, the TLHM is based on fundamental traits that
37
38 84 exhibit trade-offs and determine fitness of individuals and populations (for instance, generation
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40 85 time is a fundamental component of basic population models; and fecundity and egg size often
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42 86 exhibit trade-offs at individual and population levels; Wootton and Smith, 2014), suggesting that
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44 87 it may also apply at the population level; however, few studies have investigated intraspecific
45
46 88 trait variation among fish populations in relation to hydrologic variability. The application of
47
48 89 simple models like the TLHM or other habitat template approaches (Southwood, 1988) does not
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50 90 reflect the full complexity of factors affecting population life history and does not determine a
51
52 91 definitive mechanism for any relationships (Stearns, 1992). Yet such an application could prove
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3 92 useful in identifying potential selective environmental factors (Endler, 1986) in the absence of
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5 93 the more detailed, but difficult-to-acquire, information on age-structured mortality required of
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8 94 demographic life history theory (Stearns, 1992). Further, using population-level studies to
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10 95 confirm or refute trends from assemblage-level studies could suggest the relative merits and
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12 96 generality of the proposed mechanisms or assumptions underlying trait-environment
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15 97 relationships.

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17 98 Our specific objectives were to: 1) determine if population-level variation in life history
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19 99 traits follows assemblage-level TLHM findings; and 2) determine if predictions of the TLHM in
20
21 100 relation to flow regime apply at the population level for three stream fish species. We
22
23 101 hypothesized that: 1) intraspecific variation would be oriented similarly to the assemblage-level
24
25 102 TLHM; and 2) hydrologic variability would influence life history traits of populations as
26
27 103 predicted by the TLHM. Specifically, we hypothesized that flow variability would promote
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29 104 opportunistic traits (small size at maturity), that flow predictability/stability would promote
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31 105 equilibrium traits (large egg size), and that flow seasonality would promote periodic traits (high
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33 106 fecundity) (Table 1).

34 107 **METHODS**

35 108 *Species selection*

36
37 109 Three study species were selected based on broad geographic distributions in the Central
38
39 110 Lowlands of North America, potentially high relative abundances, and diverse ecologies: red
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41 111 shiner (*Cyprinella lutrensis*; Family Cyprinidae), bluntnose minnow (*Pimephales notatus*;
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43 112 Family Cyprinidae), and orangethroat darter (*Etheostoma spectabile*; Family Percidae). The red
44
45 113 shiner is a habitat generalist most abundant in low-gradient streams and rivers. This species
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47 114 spawns adhesive eggs in gravel riffles from spring to fall, usually peaking in June-July in the
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3 115 Midwest (Robison and Buchanan, 1988). Most individuals are mature by their second summer
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5 116 (Boschung and Mayden, 2004). The species is likely a fractional spawner, laying up to 19
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8 117 clutches/season in captivity (Boschung and Mayden, 2004). The bluntnose minnow occupies
9
10 118 mid-water column and near-benthic areas and lays eggs in rock crevices where eggs are
11
12
13 119 protected by males. Females, mature by age one, are fractional spawners and produce up to 4200
14
15 120 eggs/season during late spring-summer (Boschung and Mayden, 2004). The orangethroat darter
16
17 121 inhabits runs, pools, and riffle margins and spawns in riffles, with eggs buried in gravel and
18
19 122 receiving no parental care; females may spawn with multiple males per season during spring-
20
21 123 early summer and are mature by age one (Etnier and Starnes, 1993; Pflieger, 1997). Based on
22
23 124 species-level trait data, all three species would be classified as relatively opportunistic strategists
24
25 125 within the TLHM, having relatively short generation time, although parental care by bluntnose
26
27 126 minnow makes it more closely affiliated with the equilibrium strategy (Winemiller and Rose,
28
29 127 1992; MGB, unpublished).

33 34 128 *Site selection*

35
36 129 We selected a set of 'reference' USGS stream gages (Falcone *et al.*, 2010) that coincided with
37
38 130 probable locations of target species (see Appendix S1 for details). Final sampling locations
39
40 131 containing the target species were all within the Mississippi-Ohio River watershed (Figure 2;
41
42 132 Appendix S1). Of the sites sampled, we obtained reproductive individuals from seven
43
44 133 populations of red shiner, eight populations of orangethroat darter, and 14 populations of
45
46 134 bluntnose minnow (Appendix S1).

49 50 135 *Hydrologic variables and measurement*

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53 136 Predictions of the TLHM focus on environmental variability, stability, and predictability.
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55 137 Because of the importance of flow regime to stream ecosystems, communities, and populations,
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3 138 these predictions have largely been operationalized as variability, stability, and
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6 139 predictability/seasonality of the flow regime in studies of stream fishes. We selected hydrologic
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8 140 metrics that highlight these aspects based on two recent assemblage-level studies (Mims and
9
10 141 [Olden, 2012, 2013](#)) in order to compare results (Table 1). Annual coefficient of variation of daily
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12 142 flow (*annCV*) and the high pulse count (*HPC*) were used as measures of flow variability.
13
14 143 Colwell's flow predictability index (*FlowPred*; Colwell, 1974) and the base flow index (*BFI*)
15
16 144 were used as measures of flow predictability/stability. Flow constancy divided by predictability
17
18 145 (*ConstPred*; Colwell, 1974) and high pulse duration (*HPD*) were used as measures of flow
19
20 146 seasonality. Additionally, mean daily discharge (*meanQ*) was used to measure flow magnitude
21
22 147 due to previous findings of discharge-life history relationships (Table 1). All indices were
23
24 148 calculated using Indicators of Hydrologic Alteration software (Richter *et al.*, 1996) based on
25
26 149 medians using all years of data with <10 missing days for each gage through 2012, the year
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28 150 prior to fish sampling (Appendix S1).
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34 151 We evaluated two variables for additional influences on life history traits due to expected
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36 152 relationships from the literature: latitude and genetic divergence (Appendix S2). Latitude is
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38 153 correlated with temperature, ecosystem productivity, and other variables known to influence life
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40 154 history evolution (e.g., Leggett and Carscadden, 1978; Fleming and Gross, 1990) and served as a
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42 155 test of broader geographic patterns unrelated to flow regime. We decided whether to include
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44 156 latitude in our models by assessing individual impact on traits prior to final model testing and
45
46 157 included it if significantly related to at least one life history trait for a species ($p < 0.05$). Latitude
47
48 158 was included in bluntnose minnow and red shiner models based on significant regressions
49
50 159 (Appendix S2). Life history traits may also be influenced more by evolutionary history than local
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52 160 environmental conditions (Stearns, 1992); therefore, we evaluated the effect of genetic
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3 161 divergence on traits for orangethroat darter using published cytochrome b gene data (Bossu *et*
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5 162 *al.*, 2013) and a Mantel test between raw genetic and life history distances (cf. Olden and
6
7 163 Kennard, 2010; see Appendix S2). Based on this test, genetic divergence was not significantly
8
9 164 related to life history differences among populations (Appendix S2). Detailed phylogeographic
10
11 165 information was unavailable for the other species so we used stream distance as a potential
12
13 166 correlate of genetic divergence. Mantel tests were also non-significant for the minnow species
14
15 167 (Appendix S2). Due to this apparent lack of phylogenetic signal, we did not correct for
16
17 168 evolutionary history in subsequent analyses (Diniz-Filho *et al.*, 2012).

169 *Fish sampling*

170 Fishes were sampled from a 100 m reach within 1 km of USGS gage locations using a
171 seine (3.05 x 1.22 m) and backpack electrofishing unit (Smith-Root LR-24, Vancouver, WA).
172 Sampling was aimed at study species and ceased when approximately 30 adult females of each
173 species were obtained or when several successive sampling efforts (seine hauls or seine with
174 electrofishing) produced no additional target individuals. Sampling occurred usually once
175 seasonally as appropriate to target peak spawning for study species (spring for orangethroat
176 darter, late summer for cyprinids). Most sites were sampled in 2013 or 2014, and sometimes in
177 both years in an attempt to obtain more mature individuals (Appendix S1). Fish were euthanized
178 using MS-222 (300 mg/L), fixed in 10% formaldehyde, and transferred to 70% ethanol for
179 examination in the laboratory. While ethanol does cause size reduction of ova (Frimpong and
180 Henebry, 2012), the same procedure was conducted on all individuals and thus would not affect
181 comparisons.

182 *Life history trait variables and measurement*

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3 183 A limited number of life history variables were measured on mature females to test
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6 184 TLHM predictions. We measured mean oocyte diameter to capture the parental investment
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8 185 (equilibrium) axis, number of mature oocytes to capture the fecundity (periodic) axis, and
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10 186 smallest size of a mature female to capture the generation time (opportunistic) axis of the TLHM.

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13 187 Ovaries were extracted and classified according to the external staging method of Heins,
14
15 188 which separates females and oocytes into maturity stages based on oocyte size, coloration, yolk
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17 189 condition, and physical location in the ovum (Appendix S3) (e.g., Heins and Rabito, 1986; Heins
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19
20 190 and Baker, 1993). The diameters of 10 mature, ripening, or ripe oocytes were measured for each
21
22 191 individual using digital microscope photography (Leica MZ 9.5 stereomicroscope, Leica DFC
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24 192 320 camera; Leica Microsystems, Buffalo Grove, IL, USA) and ImageJ software (NIH,
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26
27 193 Washington, D.C.) at 150x magnification. Because most preserved oocytes were not spherical,
28
29 194 large and small axes of each oocyte were averaged (Heins and Rabito, 1988). Based on repeated
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31 195 measurements (n=5) of 10 randomly selected oocytes, measurement variance was low, ranging
32
33 196 from 3.8×10^{-6} to 2.7×10^{-4} mm. The number of mature and ripening oocytes was counted to
34
35 197 measure clutch size as an estimate of batch fecundity for each female (Heins and Rabito, 1986;
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37 198 Heins and Baker, 1993); however, ripe females were not included in counts because they could
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39 199 have already released some of the clutch before capture (Heins and Baker, 1993). Because
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43 200 advanced stage oocytes more closely correspond to the size of oocytes released during spawning,
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45 201 we used only ripening and ripe oocytes to estimate egg size for orangethroat darter and bluntnose
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47 202 minnow (Heins and Baker, 1988); however, because not all populations of red shiner had
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49 203 females at these stages, we used mature oocytes in analyses for this species. Females with mature
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51 204 oocytes were identified and the smallest standard length (SL) was recorded as a measure of
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53 205 minimum size at maturity (minSL_{mat}), a proxy for generation time (Winemiller and Rose, 1992;
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3 206 Wootton, 1998). Although interannual variation in egg size and fecundity are important aspects
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5
6 207 of life history (Wootton, 1998), for the purposes of this study we combined samples from 2013
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8 208 and 2014 within populations when available because our focus was on variation among
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10 209 populations. Trait values were divided by SL to correct for differences in size among populations
11
12 210 and correlations between size and other traits, with average individual size-corrected values for
13
14 211 fecundity and egg size (individual trait/individual SL) and minSLmat divided by average
15
16 212 population SL.

213 *Statistical analyses*

214 We first evaluated variation in fecundity, egg size, and SL within and among populations
215 using one-way ANOVA (Type III SS) in the R package “car.” Then, for each species, we used
216 multiple linear regression to predict life history traits from flow and latitude (if applicable). We
217 used principal components analysis (PCA) on flow variables to reduce the number of variables
218 for subsequent regression models (Appendix S4), evaluating each principal component (PC) axis
219 based on a broken stick model for interpretability (Jackson 1993) and scree plots. Interpretable
220 PC axes were used in subsequent regression models, which are described below.

221 The multiple linear regression models, combined with multi-model inference based on
222 small sample size Akaike information criteria (AICc) scores, were used to examine relationships
223 between life history traits and flow variables, with each of the three size-corrected life history
224 traits as the dependent variable and flow PCAs (and latitude, if appropriate) as independent
225 variables (ln-transformed). We evaluated all possible combinations of variables in linear models
226 for comparison (including intercept-only model) using the MuMIn package in R. The number of
227 models for each species-trait combination differed based on whether there were two or three flow
228 PCs and whether latitude was included in models (4 models for each life history trait for

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3 229 orangethroat darter, 8 per trait for red shiner, and 16 per trait for bluntnose minnow). Models
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6 230 were compared using AICc scores, with models within $\Delta 2$ of the lowest AICc considered
7
8 231 plausible (Burnham and Anderson, 2002). All size-corrected life history variables were ln-
9
10 232 transformed and models were evaluated to ensure they met assumptions of normality and
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12 233 homogeneity of variance. Traits were scaled to a common axis (0-1; with the inverse of
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14
15 234 minSLmat used to capture the opportunistic axis), and relationships were visualized using
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17 235 ternary plots (SigmaPlot, Systat Software Co., San Jose, CA).

19
20 236 We also conducted PCA for size-corrected, ln-transformed life history traits to evaluate
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22 237 trade-offs in relation to the TLHM. For the life history PCAs, we selected the first two PCs for
23
24 238 all species to capture the major variation and trade-offs in traits even if the second axis did not
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26
27 239 explain more variation than a single variable according to a broken stick model. We examined
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29 240 life history PCAs to determine if trait relations in multivariate space corresponded to the TLHM
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31 241 (Winemiller and Rose, 1992).

32 242 **RESULTS**

33 243 *Population-level and species-level trait variability*

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36 244 Fecundity differed significantly among populations for orangethroat darter ($F_{7,194}=31.70$,
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38 245 $P < 0.001$; raw site means \pm SE: $50.2 \pm 4.3 - 163.7 \pm 12.8$), red shiner ($F_{6,61}=2.54$, $P=0.03$; means:
39
40 246 $221.7 \pm 24.7 - 475.0 \pm 132.0$), and bluntnose minnow ($F_{13,84}=2.60$, $P < 0.01$; means: $161 \pm 17.5 -$
41
42 247 433 ± 82.5 ; Appendix S5). Despite the smaller differences among populations, egg size also
43
44 248 differed significantly among populations for orangethroat darter ($F_{7,166}=20.64$, $P < 0.001$;
45
46 249 population means: $1.02 \pm 0.008 - 1.17 \pm 0.008$ mm), red shiner ($F_{6,25}=2.74$, $P=0.03$; means:
47
48 250 $0.82 \pm 0.02 - 0.90 \pm 0.005$ mm), and bluntnose minnow ($F_{13,69}=4.94$, $P < 0.001$; means: $0.92 \pm 0.02 -$
49
50 251 1.14 ± 0.13 mm; Appendix S5). Differences in standard length of mature individuals were
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borderline among populations of red shiner ($F_{6,61}=2.15$, $P=0.06$; population means: $36.7\pm 1.16 - 45.1\pm 1.4$ mm) but did differ for orangethroat darter ($F_{7,194}=9.44$, $P<0.0001$; means: $32.3\pm 0.59 - 38.7\pm 0.54$ mm) and bluntnose minnow ($F_{13,84}=6.05$, $P<0.0001$; means: $36.8\pm 0.90 - 55.7\pm 1.05$ mm) populations (Appendix S5). Size-corrected fecundity and egg size also differed significantly ($p < 0.05$) among populations for all species, except that differences in fecundity among bluntnose minnow populations were borderline ($P= 0.06$; Appendix S5).

Life history relationships with flow regime

Flow PCs explained moderate to substantial portions of variation in some life history traits for all three species examined based on the most informative models ($R^2=0.15-0.78$; Tables 2-4; only models within $\Delta AICc=2$ of lowest $AICc$ are discussed). For fecundity in red shiner, the intercept-only model was ranked highest based in $AICc$; however, a model showing a negative relationship with flow PC2 (negative: HPD, HPC) was ranked second and within $\Delta AICc=2$ of the intercept model (Table 2; Figure 3). The top models for egg size (within $\Delta AICc=2$) showed positive relationships with flow PC1 (positive: BFI, FlowPred; negative: annCV) and latitude, with both models explaining $>70\%$ of the variation in egg size. For minSLmat, the intercept-only model was ranked best, but a model showing a negative relationship with flow PC1 (positive: BFI, FlowPred; negative: annCV) was ranked second (Table 2; Figure 3).

In bluntnose minnow, fecundity was positively related to latitude (best model) and negatively related to flow PC1, higher values of which represented less seasonal flows (lower HPD, higher ConstPred), and flow PC2 (positive: annCV; negative: BFI; Table 3; Figure 4). For egg size, the intercept-only model was ranked best but two models within $\Delta AICc=2$ showed a positive relationship with flow PC2 (positive: annCV; negative: BFI) and a negative relationship with latitude (Table 3; Figure 4). For minSLmat, the intercept-only model was also ranked as

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3 275 best, but a model with a positive relationship with flow PC3 (positive: meanQ) was within
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5 276 $\Delta AICc=2$ (Table 3; Figure 4).
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8 277 In orangethroat darter, fecundity was positively related to flow PC2 (positive: HPD;
9
10 278 negative: annCV); this model had substantially lower weight than the intercept-only model but
11
12 279 was within $\Delta AICc=2$ of the best-ranked model (Table 4; Figure 5). The intercept-only model
13
14 280 also had the best ranking among models for egg size, with the second-ranked model showing a
15
16 281 positive relationship with flow PC1 (positive: BFI; negative: HPC, FlowPred; Table 4; Figure 5)
17
18 282 that also had substantially lower weight but was within $\Delta AICc=2$ of the best-ranked model.
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21
22 283 Among models for minSLmat, the intercept-only model was the best-ranked, but the model
23
24 284 showing a positive relationship with flow PC2 (positive:HPD; negative: annCV) had similar
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26 285 weight (0.45) to the intercept-only model (0.51) and was within $\Delta AICc=2$ of the best-ranked
27
28 286 model (Table 4).
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30

31 287 *Life history trait variability and relationships*

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34 288 Life history traits along the first two PC axes largely mirrored established life history
35
36 289 trade-offs across fish species based on the TLHM (Figure 6; Appendix S4). We interpreted PC1
37
38 290 as an equilibrium-to-periodic axis for all species, with the periodic traits of high fecundity and
39
40 291 large minSLmat loading at the positive end and the equilibrium trait of large egg size at the
41
42 292 negative end of the axis (Figure 6). We interpreted PC2 as an opportunistic to periodic axis for
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44 293 all species, with the opportunistic trait of small minSLmat loading on the negative end of the
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46 294 axis, and the periodic traits of high fecundity or large minSLmat loading on the positive end
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48 295 (Figure 6).
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51 296 **DISCUSSION**

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3 297 Our results suggest that the trait-based life history trade-offs and strategies of the TLHM
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6 298 may apply at the population level for three common fish species and that some of the predicted
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8 299 effects of flow regime variability and predictability mirror those found at the assemblage level
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11 300 (Mims and Olden, 2012, 2013), suggesting consistent mechanisms. Trade-offs between periodic
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13 301 (large body size, high fecundity) and opportunistic traits (small size at maturity) and between
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15 302 opportunistic and equilibrium traits (large egg size) largely described the life history investment
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17 303 of populations as predicted by the TLHM. While we did select a small number of traits to
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19 304 coincide with the TLHM, there was no *a priori* reason for these traits to ordinate in a similar
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21 305 fashion.
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24 306 Although the population-level life history traits examined in this study aligned well with
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26 307 the assemblage-based TLHM, the predicted relationships between hydrology and life history
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28 308 traits had variable support. As predicted by the TLHM, populations of bluntnose minnow and
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30 309 orangethroat darter that experience more seasonal (high HPD) and less variable (low CV, HPC)
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32 310 flows had higher fecundity. Also as predicted, sites with greater flow stability (BFI) had
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34 311 populations of red shiner and orangethroat darter with larger eggs. Orangethroat darter
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36 312 populations from low-variability sites and red shiner populations from more stable sites also had
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38 313 larger minSLmat, as predicted. However, counter to TLHM predictions, seasonality and
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40 314 variability measures were correlated in among red shiner sites, leading to a positive relationship
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42 315 between fecundity and HPD/HPC. Higher variability was also associated with larger eggs in
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44 316 bluntnose minnow populations, counter to TLHM predictions. Overall, these relationships
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46 317 suggest that, in many cases, flow regime (or some correlated variable) is associated with life
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48 318 history traits of populations in some ways as predicted by the TLHM and assemblage-level
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50 319 studies (Mims and Olden, 2012).
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3 320 Support for TLHM flow-trait associations varied by species, suggesting species-level
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6 321 differences in behavior could influence how organisms experience flow variation. Both minnow
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8 322 species have adhesive eggs, with red shiner often described as crevice spawning but utilizing
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10 323 various substrates and bluntnose minnow attaching eggs to the underside of rocks where they are
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12 324 actively guarded. The orangethroat darter buries eggs in gravel interstices and also does not
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15 325 defend the clutch (Boschung and Mayden, 2004). The different responses of egg size to flow
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17 326 regime in these species (bluntnose minnow: larger eggs with more variable flow; others: larger
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19 327 eggs with more stable flow;) could be a result of different spawning behavior, with more
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21 328 physical protection afforded to bluntnose minnow clutches and eggs of the other two species left
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23 329 at risk of reduced hatching in variable flows (Durham and Wilde, 2006). Larger eggs, which
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25 330 produce larger offspring may be favored under variable flows if mortality at the egg stage is
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27 331 reduced through protection. Flow variables for future trait-environment prediction should be
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29 332 carefully selected as species experience flow variability differently based on life history and
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31 333 behavioral differences (Poff and Ward, 1990; Beachum *et al.*, 2015).

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36 334 Identifying mechanisms underlying flow-trait relationships is made difficult by trade-offs
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38 335 among traits, and determining which traits could be under selection, or the role of phenotypic
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40 336 plasticity in trait responses, is quite challenging (Wootton and Smith, 2014). For instance, egg
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42 337 size appears inversely correlated with fecundity in our study species, as is commonly the case
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44 338 due to physiological and geometric limits; thus responses of one trait may be the result of
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46 339 selection on another (Wootton and Smith, 2014). The fact that egg size and fecundity generally
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48 340 did not respond to the same flow regime components (except in bluntnose minnow, Table 3)
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50 341 suggests that our patterns may not be merely the result of trade-offs between these traits. Recent
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52 342 studies of fish life history traits have documented substantial local adaptation with a genetic
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3 343 basis, but particular traits such as egg size may exhibit extreme plasticity (Torres Dowdall *et al.*,
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5 344 2012; Wootton and Smith, 2014).
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8 345 Our estimates of life history traits and flow relationships were inevitably influenced by
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10 346 several factors including small sample sizes and assumptions about measured traits. Small
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12 347 sample sizes are typical for multi-site life history studies of small-bodied fishes over broad
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14 348 geographic regions, and timing sampling effort to spawning at many of sites was difficult,
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16 349 especially for cyprinids. Further, the small size of the streams sampled and the reliance on USGS
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18 350 gages limited the number of available sampling locations. Small sample sizes could influence
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20 351 trait estimates and increase sample variability. Minimum SL at maturity is likely to change with
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22 352 increased sampling because of its dependence on capturing the smallest reproductive individual
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24 353 in a population; however, this trait was correlated with median SL in all species, suggesting that
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26 354 it might be more resilient to sample size effects. The consistency of slopes between the full
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28 355 dataset and the dataset with small samples (<4 individuals) removed in all but one case suggests
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30 356 that our results may be somewhat robust to small sample sizes (Appendix S6). However, related
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32 357 to issues of small sample size, the presence of outliers, particularly in two of the three important
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34 358 models for red shiner (population RCNE in both cases), appeared to drive relationships and
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36 359 should be considered.
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43 360 Although most of the study species lay multiple clutches in a season, we were limited to
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45 361 using batch fecundity due to difficulty in measuring number of clutches per season (Winemiller
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47 362 and Rose, 1992). Batch fecundity is thought to closely correlate with lifetime fecundity (Roff,
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49 363 1992) and is frequently used to characterize fecundity and life history patterns (Winemiller and
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51 364 Rose, 1992); however, the actual relationship for the study species is unknown. If batch
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53 365 fecundity is not strongly correlated with annual or lifetime fecundity in the study species, the
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3 366 relationships we report may not represent important life history trade-offs or environmental
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5 367 variation. We also used egg size to represent parental investment, and thus an assumption of our
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8 368 study is that parental care behavior remains constant across populations. Increasing parental care
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10 369 behavior may be a more viable evolutionary strategy than increasing fecundity or egg size due to
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12 370 evolutionary constraints of small body size in many stream fishes (Winemiller and Rose, 1992);
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14 371 however, parental care may be less evolutionarily labile than the life history traits in our study
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16 372 (Sternberg and Kennard, 2014). Among the study species, bluntnose minnow exhibits parental
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18 373 care, and this could confound attempts to evaluate investment per progeny in relation to flow
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20 374 regime using only egg size.
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24 375 Our findings combined with those of other studies suggest – whether due to phenotypic
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26 376 plasticity, natural selection, or a combination – intraspecific trait variation in fishes is high
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28 377 (Blanck and Lamouroux, 2006; Frimpong and Angermeier, 2010). Although we were unable to
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30 378 undertake a full assessment of intra- versus inter-specific trait variability, at least one trait per
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32 379 species exhibited substantial variation at the population level that rivaled variability at the family
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34 380 or congeneric level (e.g., compare data in FishTraits, Frimpong and Angermeier, 2009). Such
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36 381 high variability within species could greatly affect community-level trait studies, which normally
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38 382 assign mean trait values to species (Albert *et al.*, 2010; Frimpong and Angermeier, 2010). While
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40 383 the three species studied are known to be widely-distributed and might therefore be expected to
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42 384 exhibit more trait variation than restricted-range species, they are common members of fish
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44 385 assemblages in eastern and central North America. Therefore, while not necessarily suggestive of
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46 386 intraspecific trait variability in fishes as a whole, such variation could have significant bearing on
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48 387 trait models and should be investigated more broadly in fishes.
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3 388 The potential for high intraspecific trait variation, coupled with the fact that the TLHM
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6 389 explained life history trait variation at the population level, suggests that efforts to synthesize
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8 390 environmental filtering or habitat template models with demographic life history theory, which is
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10 391 currently lacking, could be valuable (Wootton, 1998). This could be accomplished by linking
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12 392 age- or size-specific mortality or its correlates to key environmental features like flow regime or
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14 393 habitat variability from major template theories like the TLHM or River Habitat Template
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16 394 (Townsend and Hildrew, 1994). Once environmental factors are known to be selective,
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18 395 demographic theory could be used to make new predictions about the effects of the environment
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20 396 on life history traits. With testing and refinement of these predictions, knowledge of how and
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22 397 why individual species respond to environmental conditions and gradients could then improve
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24 398 understanding of community assembly and change (Matthews, 1998).

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29 399 The ability to predict trait responses to environmental variation has major implications
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31 400 for species and community persistence in the face of continuing habitat destruction and climate
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33 401 change. As functional traits, the life history parameters of the TLHM largely determine
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35 402 individual performance and population viability. For example, there is evidence that larger eggs
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37 403 produce larger offspring (Gale, 1986; Marsh, 1986; Kamler, 2005), which can be stronger and
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39 404 have higher survival under a variety of conditions (Marsh, 1986; Harvey, 1987). Our results
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41 405 suggest that larger eggs and offspring are associated with more stable flow conditions in some
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43 406 species (red shiner, orangethroat darter); thus, increasing flow variability from climate change, as
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45 407 predicted for the Midwestern U.S. (Wuebbles and Hayhoe, 2004), could promote smaller
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47 408 offspring with reduced survival. Trait-environment models that are well-supported at multiple
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49 409 levels of biological organization could help us understand how changing flow or temperature
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51 410 regimes will impact population and community viability and the sustainability of the valuable
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3 411 ecosystem services that they, and their natural variability, support (Daily, 1997; Luck *et al.*,
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5 412 2003).

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590 Table 1. Hydrologic metrics and predicted impacts of their increase on life history strategy and
 591 traits used in this study (modified from Mims & Olden 2012). Letters after metrics refer to flow
 592 regime component measured by metric: V = variability, P = predictability, S = seasonality. + =
 593 predict positive relationship between flow variable and traits; - = predict negative relationship
 594 between flow variable and traits; 0 = predict no relationship between flow variable and traits.

Hydrologic parameter	Abbreviation	Description	Predicted relationship w/ life history strategy		
			Opportunistic (small size at maturity)	Periodic (high fecundity)	Equilibrium (large egg size)
Annual coefficient of variation (V)	AnnCV	Standard deviation of all daily flow values divided by mean annual flow	+	-	-
High pulse count (V)	HPC	Number of flows >75 th percentile each year	+	-	-
Base flow index (P)	BFI	7-day minimum flow/mean flow for year	-	0	+
Flow predictability (P)	FlowPred	Constancy (measure of temporal invariance) + contingency (measure of periodicity)	-	+	+
Constancy/predictability (S)	Const/Pred	Constancy/(constancy + contingency)	0	-	+
High pulse duration (S)	HPD	Median duration of flows >75 th percentile	-	+	0
Mean discharge ¹	MeanQ	Average of daily flows over study period	-?	+	+/-

¹ Predictions for meanQ are based on other literature sources (Heins and Baker, 1987; Heins and Rabito, 1988; Heins, 1991; Machado *et al.*, 2002; Cattaneo, 2005a, 2005b; Morrongiello *et al.*, 2012). Prediction for Opportunistic strategy based on correlation with periodic traits (larger size and size at maturity).

595 Table 2. Regression model selection results for fecundity, egg size, and minimum SL at maturity (minSLmat) for all species. Bold
 596 models indicate those within $\Delta AICc=2$ of lowest AICc. For red shiner and bluntnose minnow, only four best-ranked models shown for
 597 each trait of a possible eight and 16 models, respectively.

Model	R ²	df	logLik	AICc	$\Delta AICc$	weight	Model Coefficients				
							Intercept	Latitude	flowPC1	flowPC2	flowPC3
<u>Red Shiner</u>											
Fecundity (intercept)	0.00	2	-0.063	7.1	0.00	0.62	0				—
Fecundity ~ FlowPC2	0.56	3	2.795	8.4	1.28	0.327	0			-0.747	—
Fecundity~FlowPC1	0.13	3	0.413	13.2	6.05	0.030	0			-0.357	—
Fecundity~Latitude	0.01	3	-0.043	14.1	6.96	0.019	0		-0.076		—
Egg size~FlowPC1	0.78	3	11.119	-8.2	0.00	0.638	0			0.885	—
Egg size~Latitude	0.72	3	10.209	-6.4	1.82	0.257	0		0.848		—
Egg size (intercept)	0.00	2	5.763	-4.5	3.71	0.100	0				—
Egg size~FlowPC2	0.00	3	5.772	2.5	10.70	0.003	0			0.051	—
MinSLmat (intercept)	0.00	2	3.724	-0.4	0.00	0.476	0				—
MinSLmat~FlowPC1	0.60	3	6.950	0.1	0.55	0.362	0			-0.776	—
MinSLmat~Latitude	0.49	3	6.048	1.9	2.35	0.147	0		-0.697		—
MinSLmat~FlowPC2	0.02	3	3.778	6.4	6.89	0.015	0			-0.124	—
<u>Bluntnose Minnow</u>											
Fecundity~Latitude	0.43	3	-0.428	9.3	0.00	0.325	0		0.657		—
Fecundity~FlowPC1+2	0.54	4	1.111	10.2	0.97	0.200	0			-0.422	-0.604
Fecundity~FlowPC2	0.37	3	-1.196	10.8	1.54	0.150	0				-0.604

Fecundity ~Lat+FlowPC2	0.49	4	0.270	11.9	2.65	0.086	0	0.457	-0.306	
Egg size (intercept)	0.00	2	14.540	-24.0	0.00	0.283	0			
Egg size~FlowPC2	0.17	3	15.823	-23.2	0.74	0.195	0		0.409	
Egg size~Latitude	0.15	3	15.688	-23.0	1.01	0.171	0	-0.389		
Egg size~FlowPC1	0.09	3	15.173	-21.9	2.04	0.102	0	0.294		
MinSLmat (intercept)	0.00	2	17.167	-29.2	0.00	0.300	0			
MinSLmat~FlowPC3	0.16	3	18.355	-28.3	0.93	0.188	0		0.395	
MinSLmat~FlowPC2	0.07	3	17.654	-26.9	2.34	0.093	0		-0.259	
MinSLmat~FlowPC1	0.06	3	17.620	-26.8	2.40	0.090	0	-0.250		
<u>Orangethroat Darter</u>										
Fecundity (intercept)	0.00	2	-2.519	11.4	0.00	0.681	0	—	—	
Fecundity~FlowPC2	0.38	3	-0.625	13.3	1.81	0.275	0	—	0.614	
Fecundity~FlowPC1	0.00	3	-2.514	17.0	5.59	0.042	0	—	0.033	
Fecundity~FlowPC1+2	0.38	4	-0.618	22.6	11.13	0.003	0	—	0.033	
Egg size (intercept)	0.00	2	10.650	-14.9	0.00	0.661	0	—	—	
Egg size~FlowPC1	0.37	3	12.513	-13.0	1.87	0.259	0	—	0.610	
Egg size~FlowPC2	0.14	3	11.241	-10.5	4.42	0.073	0	—	-0.371	
Egg size~FlowPC1+2	0.51	4	13.501	-5.7	9.23	0.007	0	—	0.610	
MinSLmat (intercept)	0.00	2	-13.836	-21.3	0.00	0.511	0	—	—	
MinSLmat~FlowPC2	0.49	3	16.510	-21.0	0.25	0.450	0	—	0.698	
MinSLmat~FlowPC1	0.02	3	13.916	-15.8	5.44	0.034	0	—	0.141	
MinSLmat~FlowPC1+2	0.51	4	16.667	-12.0	9.27	0.005	0	—	0.141	

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Figure Legends

Figure 1. The trilateral life history framework of Winemiller and Rose (1992). Modified from Winemiller (2005), and Mims and Olden (2012).

Figure 2. Map of study sites where mature (mature, ripening, or ripe) specimens of target species were found. For site codes and information, see Appendix S1.

Figure 3. Population life history strategies and flow-trait relationships for red shiner. (a) Ternary plot illustrating trade-offs in traits among populations. Axes scaled between 0 and 1 for the three traits (bottom axis: fecundity; right axis: egg size; left axis: inverse(minSLmat)). Solid circles represent study sites (see Appendix S1). (b) Scatterplots of flow PC-trait relationships. Asterisk indicates important relationship from multiple regression results (Table 2). Higher values of flow PC1 (lower CV), in left panels, were associated with larger eggs and smaller size at maturity. Higher values of flow PC2 (lower HPC, HPD, higher CV), on right panels, were associated with lower fecundity. Illustration of male red shiner copyright and used with permission of Joseph R. Tomelleri.

Figure 4. Population life history strategies and flow-trait relationships for bluntnose minnow. (a) Ternary plot illustrating trade-offs in traits among populations. Axes scaled between 0 and 1 for the three traits (bottom axis: fecundity; right axis: egg size; left axis: inverse(minSLmat)). Solid circles represent study sites (see Appendix S1). (b) Scatterplots of flow PC-trait relationships. Asterisk indicates important relationship from multiple regression results (Table 2). Higher values of flow PC1 (lower HPD, higher ConstPred), in left panels, were associated with lower

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3 fecundity. Higher values of flow PC2 (higher CV, HPC; lower BFI), in middle panels, were
4 associated with lower fecundity and larger egg size. Higher values of flow PC3 (higher meanQ),
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6 right panels, were associated with larger size at maturity. Illustration of male bluntnose minnow
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8 copyright and used with permission of Joseph R. Tomelleri.
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15 Figure 5. Population life history strategies and flow-trait relationships for orangethroat darter. (a)
16 Ternary plot illustrating trade-offs in traits among populations. Axes scaled between 0 and 1 for
17 the three traits (bottom axis: fecundity; right axis: egg size; left axis: inverse(minSLmat)). Solid
18 circles represent study sites (see Appendix S1). (b) Scatterplots of flow PC-trait relationships.
19
20 Asterisk indicates important relationship from multiple regression results (Table 2). Higher
21 values of flow PC1 (higher BFI, lower HPC) were associated with larger eggs. Higher values of
22 flow PC2 (higher HPD, lower CV) were associated with higher fecundity and larger size at
23 maturity. Illustration of male orangethroat darter (*E. spectabile pulchellum*) copyright and used
24 with permission of Joseph R. Tomelleri.
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39 Figure 6. Principal component plots for life history traits for (left to right) red shiner, bluntnose
40 minnow, and orangethroat darter. We interpreted PC1 as an equilibrium (negative) to periodic
41 (positive) axis for all species. We interpreted PC2 as an opportunistic (around zero) to periodic
42 (positive or negative) axis for all species. Red text associated with arrows identifies trait vectors
43 (ln-transformed, size-corrected traits). Uppercase black text identifies site scores (see Appendix
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Supplementary Material

Appendix S1. Sample and gage locations and collecting information

Appendix S2. Additional environmental and other data for study sites and evaluation for inclusion in final model sets

Appendix S3. Ovary and oocyte stages and descriptions

Appendix S4. Principal components results for flow and life history trait variable reduction

Appendix S5. Data on life history trait variability among populations

Appendix S6. Comparison of results from full datasets with results after small samples removed

For Peer Review

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3 **Population-level responses of life history traits to flow regime in three common stream fish**
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5 **species**
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8 Micah G. Bennett^{1*}, Matt R. Whiles¹, and Gregory W. Whitley^{1,2}
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12 Electronic supporting material
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The following Supporting Information is available for this article:

Appendix S1. Sample and gage locations and collecting information

Appendix S2. Additional environmental and other data for study sites and evaluation for inclusion in final model sets

Appendix S3. Ovary and oocyte stages and descriptions

Appendix S4. Principal components results for flow and life history trait variable reduction

Appendix S5. Data on life history trait variability among populations

Appendix S6. Comparison of results from full datasets with results after small samples removed

For Peer Review

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3 **Appendix S1.** Sample and gage location selection and collecting information.
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6 To limit the influence of anthropogenic flow modification, potential study reaches were selected
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8 based on proximity to “reference” USGS stream gages from the GAGES (Gages for Evaluating
9
10 Stream Flow) database ([Falcone *et al.*, 2010](#)). This database contains USGS stream gages with
11
12 discharge data from 1950-2007 and determines “reference” gage designations based on
13
14 anthropogenic modification of stream flow in the gaged watersheds, including human population
15
16 and urban/housing density and presence of dams and channelization ([Falcone *et al.*, 2010](#)).
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18 Gages within the Central Lowlands physiographic province were further selected to limit
19
20 variability based on ecoregion while still maintaining a large number of potential gages from
21
22 which to select.
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27 Reference gages were narrowed by selecting those with comparable temporal coverage
28
29 (≥ 15 years of flow data prior to 2013; $> 40\%$ overlap in period of flow record) and excluding
30
31 gages with > 10 days of missing data per year ([Kennard *et al.*, 2010](#); [Mims and Olden, 2012](#)).
32
33 Finally, the partitioning around medioids (PAM) procedure (“pam” command) in the package
34
35 “cluster” in R (R Core [Team, 2012](#)) was used to group gages based on similarity in drainage size.
36
37 PAM is a non-hierarchical clustering method that searches for representative medioids (point
38
39 nearest a multivariate centroid) among observations and assigns each observation to one of these
40
41 medioids, forming clusters ([Borcard *et al.*, 2011](#)). Three groupings were best as judged by
42
43 average silhouette width (degree of membership of an observation to a cluster) ([Borcard *et al.*,](#)
44
45 [2011](#)), and the largest group was selected ($n=31$). Particular gage sites were then selected which
46
47 spanned the range of variation in the hydrologic metrics and were likely to contain the target
48
49 species based on information from fish collections (FishNet2, Illinois Natural History Survey, U.
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51 of Kansas, Ohio State U., Indiana Dept. of Environmental Management) and the Global
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3 Biodiversity Information Facility (www.gbif.org). Final sampling locations containing the target
4
5 species were all within the Mississippi-Ohio River watershed (Figure 2; Appendix S1). Of the
6
7 sites sampled, we obtained reproductive individuals from seven populations of red shiner, eight
8
9 populations of orangethroat darter, and 14 populations of bluntnose minnow (Appendix S1).
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Table S1. Species columns contain number of individuals for fecundity and egg size estimates, respectively. Mature and ripening oocytes were combined to estimate fecundity, but only ripening and ripe oocytes were used to estimate egg size when available (except for Red Shiner; see text and Appendix S3).

Gage No ₁	Code	Site Name	Drainage	Lat	Long	Flow Years	Red Shiner (fecundity; egg size)	Bluntnose Minnow (fecundity; egg size)	Orangethroat Darter (fecundity; egg size)	Sample Years
5556500	BBIL	Big Bureau Cr., Princeton, IL	Illinois R.	41.37	-89.50	1938-2012	0;0	15;15	18;29	2013, 2014
3340800	BRIN	Big Raccoon Cr., Fincastle, IN	Wabash R.	39.81	-86.95	1958-2012	-	10;9	-	2014
3364500	CCIN	Clifty Cr., Hartsville, IN	E. Fk. White R.	39.27	-85.70	1949-2012	-	1;2	-	2014
7180500	CCKS	Cedar Cr., Cedar Point, KS	Cottonwood/upper Neosho R.	38.20	-96.82	1939-2012	6;5	8;6	38;17	2013, 2014
5503800	CCMO	Crooked Cr., Paris, MO	Salt R. (upper Mississippi R.)	39.58	-91.99	1980-2012	2;2	17;13	43;13	2013, 2014
5444000	ECIL	Elkhorn Cr., Penrose, IL	Rock R.	41.90	-89.70	1940-2012	-	14;11	-	2013, 2014
7184000	LCKS	Lightning Cr., McCune, KS	Neosho R.	37.28	-95.03	1960-2012	2;2	2;2	16;20	2014
5317200	LCMN	Little Cottonwood R., Courtland, MN	Minnesota R.	44.25	-94.34	1974-2009	-	2;1	-	2013
5507600	LCMO	Lick Cr., Perry, MO	Salt R. (upper Mississippi R.)	39.43	-91.68	1980-2012	0;0	2;1	20;40	2014
6910800	MdCKS	Marais des Cygnes R., Reading, KS	Marais des Cygnes/ Osage R.	38.57	-95.96	1970-2012	20;13	9;7	26;25	2013, 2014
7167500	OCKS	Otter Cr., Climax, KS	Fall/Verdigris R.	37.71	-96.22	1947-	2;2	6;6	21;11	2014

						2012				
3327520	PCIN	Pipe Cr., Bunker Hill, IN	Wabash R.			1969-	-	1;1	-	2013
				40.67	-86.10	2003				
6803530	RCNE	Rock Cr., Ceresco, NE	Salt Cr./ Platte R.			1941-	24;5	-	-	2013,
				41.02	-96.54	2012				2014
6889160	SCKS	Soldier Cr., Circleville, KS	Kansas R.			1965-	12;4	9;7	20;18	2014
				39.46	-95.95	2000				
3272700	SCOH	Sevenmile Cr., Camden, OH	Great Miami R.			1971-	-	2;2	-	2013
				39.63	-84.64	2000				

¹U.S. Geological Survey, www.waterdata.usgs.gov

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3 **Appendix S2.** Additional environmental and other data for study sites and evaluation for
4 inclusion in final model sets.
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9 Many environmental factors that can influence life history such as growing season,
10 temperature, and climate patterns are correlated with latitude, and several studies have found
11 significant latitudinal clines in life history traits (Leggett and Carscadden, 1978; Fleming and
12 Gross, 1990; Johnston and Leggett, 2002). Latitude was calculated for each site from Google
13 Earth (Google, Inc., Mountain View, CA) and included in final models for Bluntnose Minnow
14 and Red Shiner based on significant regressions for some traits ($p < 0.05$).
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23 Recent molecular data suggest that our sampling sites for Orangethroat Darter include
24 three distinct phylogenetic clades reflective of ancient drainage configurations, glacial refugia,
25 and dispersal events (Bossu *et al.*, 2013): a western clade (including sites CCKS, LCKS, OCKS,
26 SCKS) that included *Etheostoma spectabile pulchellum* and *E. s. squamosum*, which separated
27 from populations east of Kansas approximately 4.5 Ma during the Pliocene (Bossu *et al.* 2013);
28 two sister clades from the Osage and Marais des Cygnes rivers (including site MdCKS) and
29 lower portions of middle Mississippi River and tributaries; and a clade including upper
30 Mississippi River tributaries (including the Illinois River and presumably site BBIL in the
31 Illinois drainage and presumably sites CCMO and LCMO in the Salt River, but this drainage was
32 not sampled). Because life history traits could be influenced more by evolutionary history than
33 local environmental conditions (Harvey and Pagel, 1991; Stearns, 1992), we evaluated the effect
34 of genetic divergence on life history traits using published data on the cytochrome b (cyt b) gene
35 (Bossu *et al.*, 2013). We obtained 90 cyt b sequences used by Bossu *et al.* (2013) from GenBank
36 (<http://www.ncbi.nlm.nih.gov/genbank/>) representing all available cyt b sequences from the
37 clades listed above. Similar to Olden and Kennard (2010), we conducted a Mantel test (phytools
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3 package in R with 999 permutations) between raw genetic and life history distances (ln-
4 transformed, size-corrected values of fecundity, minSLmat, and egg diameter) based on
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6 Euclidean distances calculated in the vegan package in R. Based on this test, life history
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8 differences were not significantly related to genetic divergence among populations ($R^2=0.01$,
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14 P=0.49).

15 Detailed phylogeographic information was not available for the other study species;
16
17 however, because our study area encompasses mostly formerly-glaciated streams, we used
18
19 pairwise stream distances as a potential corollary of genetic divergence due to dispersal
20
21 limitation and isolation-by-distance. This is a feature of phylogeographic patterns in portions of
22
23 the range of some minnow species (e.g., Echelle et al. 2014) but ignores the likelihood of
24
25 dispersal from several glacial refugia (e.g., Berendzen et al. 2003; Berendzen et al. 2008) and
26
27 resulting patterns that would contradict simple isolation-by-distance. We calculated pairwise
28
29 stream distances (km) among all populations of Red Shiner and Bluntnose Minnow in ArcMap
30
31 10.2 (Network Analyst Tool) and used them in Mantel tests with trait distances among all
32
33 populations calculated as with Orangethroat Darter. For Red Shiner ($R^2=0.001$, $P=0.80$) and
34
35 Bluntnose Minnow ($R^2=0.005$, $P = 0.55$), stream distances did not significantly explain
36
37 differences in life history traits.
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Appendix S3. Ovary and oocyte stages and descriptions^a.

Stage	Description
Latent (LA)	Ovaries transparent-translucent and thin; maturing oocytes without visible yolk or with nucleus still visible
Early Maturing (EM)	Ovaries translucent to opaque and small-moderate sized; maturing oocytes are small-moderate, translucent to opaque, and with nucleus obscured by yolk
Late Maturing (LM)	Ovaries white to cream and small to greatly enlarged; maturing oocytes are moderate to large and white-cream or yellow
Mature (MA)	Ovaries cream to yellow and moderately to very enlarged; two distinct groups of oocytes present including a group of small oocytes (translucent to opaque) and a group of larger oocytes that are opaque and cream to yellow but without vitelline membrane (membrane surrounding yolk) separated from yolk
Ripening (MR)	Ovaries cream to yellow and moderately to very enlarged; two distinct groups of oocytes present including a group of small oocytes and a group of larger oocytes that are translucent or transparent with the vitelline membrane obviously separated from yolk
Ripe (RE)	Ovaries cream to yellow and moderately sized to greatly enlarged; two groups of relatively large oocytes present including a group of white-cream moderate to large maturing oocytes and a group of translucent to transparent ripe oocytes positioned toward the ovipositor with the vitelline membrane separated from yolk

^a (Heins and Rabito 1986; Heins and Baker 1993; Ross 2013)

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3 **Appendix S4.** Principal components results for flow and life history trait variable reduction.
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6 *Flow variable reduction*
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9 Many of the hydrologic variables were highly correlated based on PCA (Table 1; Figures 1-3).
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11 Flow variation across orangethroat darter populations was best explained by the first two PC
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13 axes (75% of the variation). We interpreted the first PC as a contrast between flow variability
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15 (high negative loadings of HPC) and predictability (high positive loadings of BFI); however, the
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17 other measure of predictability (FlowPred) also loaded strongly positively. We interpreted the
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19 second PC as a contrast between variability (high negative loadings of annCV) and both
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21 discharge and seasonality (high positive loadings of meanQ and HPD, negative loadings for
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23 ConstPred). Variables across red shiner populations were best explained by the first two PC axes
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25 (84% of variation; Appendix S4). We interpreted the first axis as a contrast between variability
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27 (high negative loadings of annCV) and predictability (high positive loadings of BFI and
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29 FlowPred). We interpreted the second axis as contrasting variability and seasonality (high
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31 negative loadings of HPC and HPD) with predictability (less negative or near zero loadings of
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33 BFI and FlowPred). Variables across bluntnose minnow populations were best explained by the
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35 first three PC axes (77% of variation; Table 1). We interpreted the first axis as contrasting
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37 seasonality from other metrics (high negative loadings of HPD, positive loadings for ConstPred);
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39 the second axis as contrasting predictability (high negative loadings of BFI and FlowPred) and
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41 variability (high positive loadings of annCV and HPC); and the third axis as a discharge axis
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43 (high positive loadings meanQ).
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Table 1. Principal component loadings for flow variables. Letters after variables refer to flow regime components (see Table 1): v= variability; s= seasonality; p = predictability.

Variable	Red Shiner		Bluntnose Minnow			Orangethroat Darter	
	PC1 (60.9%)	PC2 (23.3%)	PC1 (31.5%)	PC2 (28.8%)	PC3 (16.9%)	PC1 (39.4%)	PC2 (35.8%)
meanQ	-0.329	-0.357		-0.139	0.831		0.481
annCV (v)	-0.471	0.145	0.356	0.545	-0.188	-0.203	-0.503
HPC (v)		-0.606	0.362	0.302	0.473	-0.540	-0.150
BFI (p)	0.477		0.250	-0.616	-0.110	0.518	-0.169
FlowPred (p)	0.450	-0.283	0.365	-0.428		-0.554	
HPD (s)	-0.199	-0.629	-0.461	-0.131	-0.111	-0.269	0.507
Const/Pred (s)	0.447		0.573	-0.113	-0.152	-0.129	-0.456

Table 2. Principal component loadings for life history variables. All life history variables were size-corrected and ln-transformed.

Variable	Red Shiner		Bluntnose Minnow		Orangethroat Darter	
	PC1 (69.4%)	PC2 (24.5%)	PC1 (42.2%)	PC2 (32.2%)	PC1 (56.4%)	PC2 (36.1%)
Ln(Fecundity)	0.45307	0.88082	0.469583	0.785903	0.711943	0.192302
Ln(Egg Size)	-0.61532	0.420524	-0.68203	0.033548	-0.70099	0.25179
Ln(min SL @ maturity)	0.645063	-0.21752	0.560647	-0.61744	0.041746	0.948484

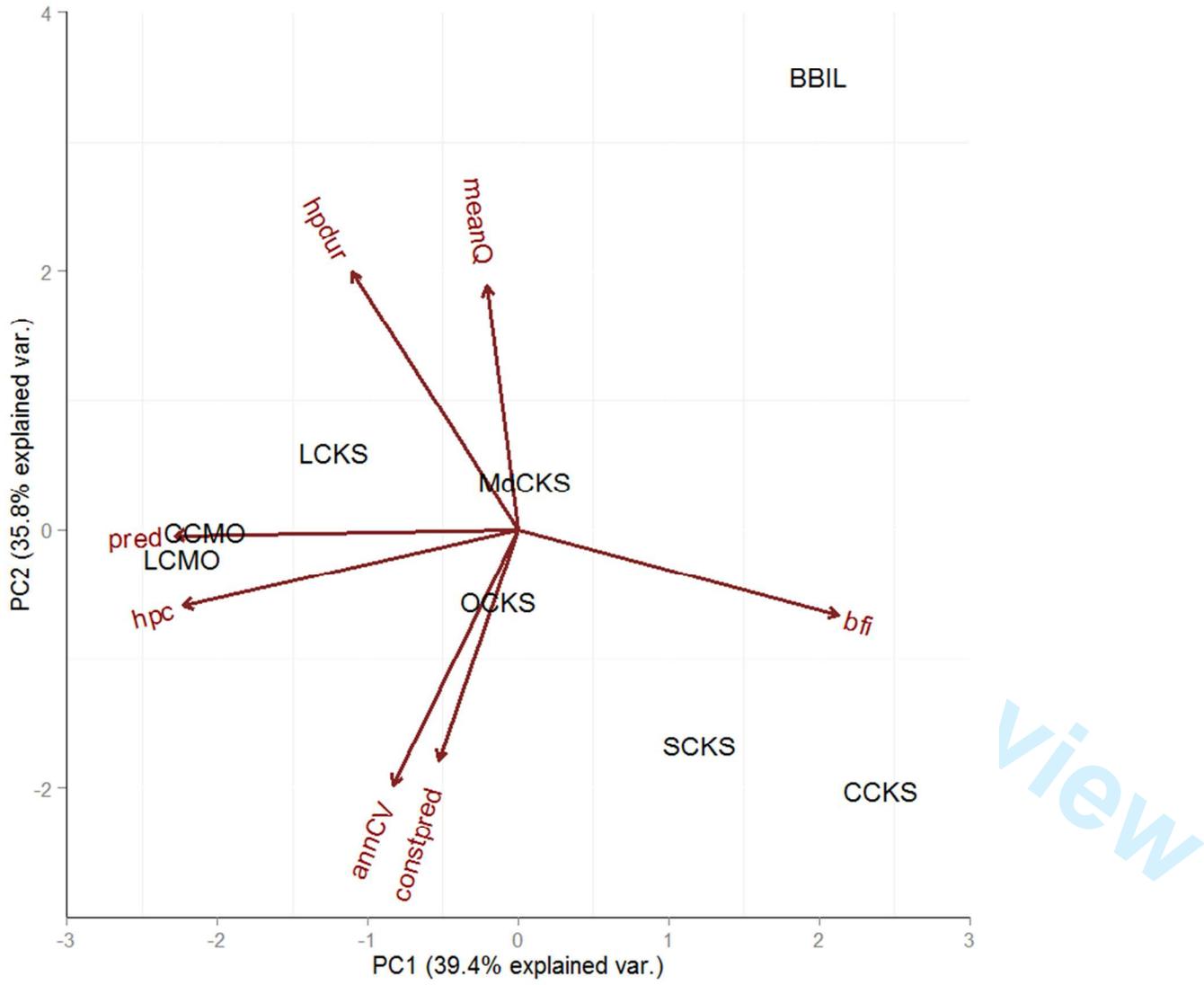


Figure 1. Flow PCA for Orangethroat Darter. Black text shows site scores. Red arrows and text highlight flow variable vectors.

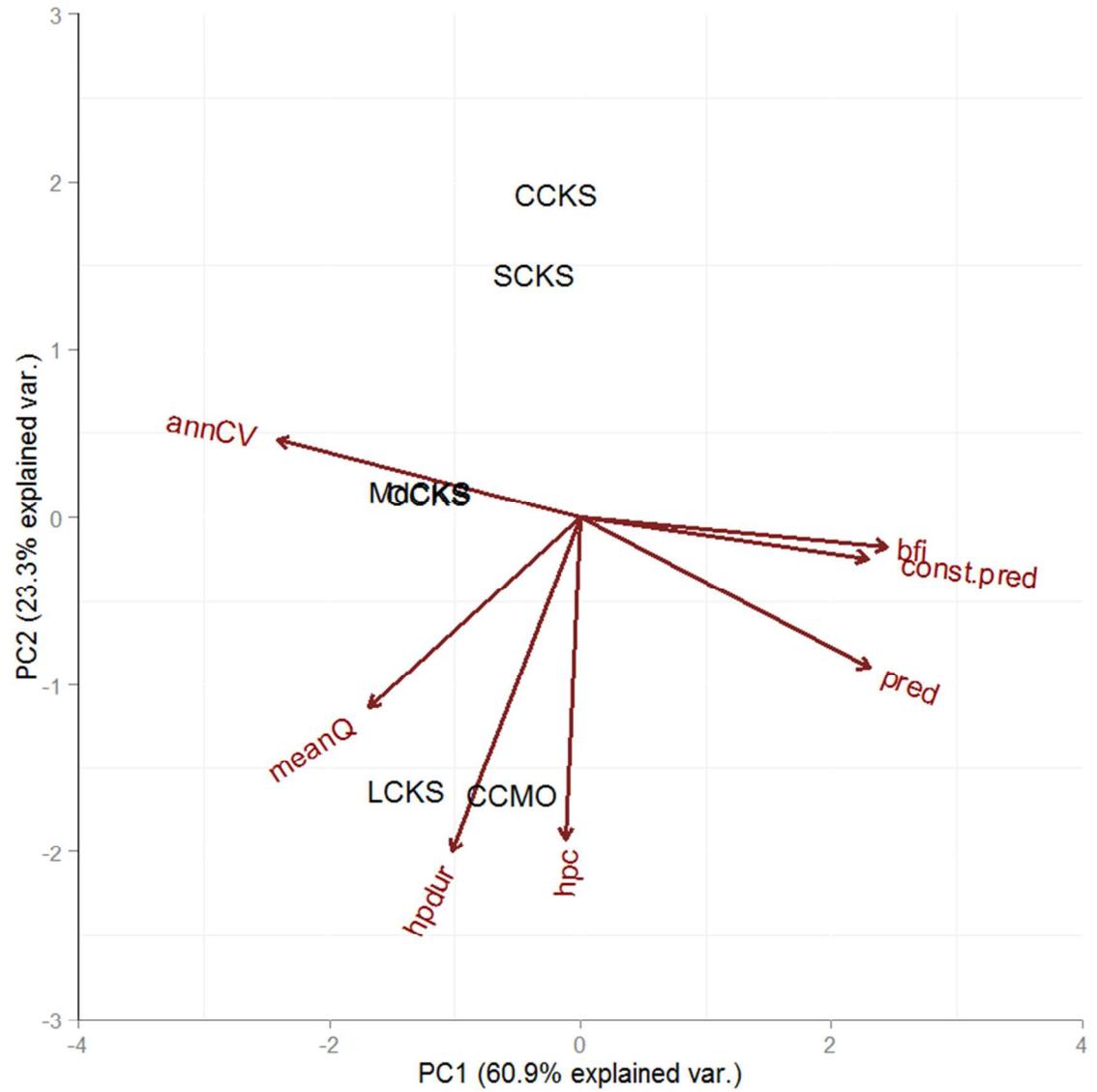


Figure 2. Flow PCA for Red Shiner. Black text shows site scores. Red arrows and text highlight flow variable vectors.

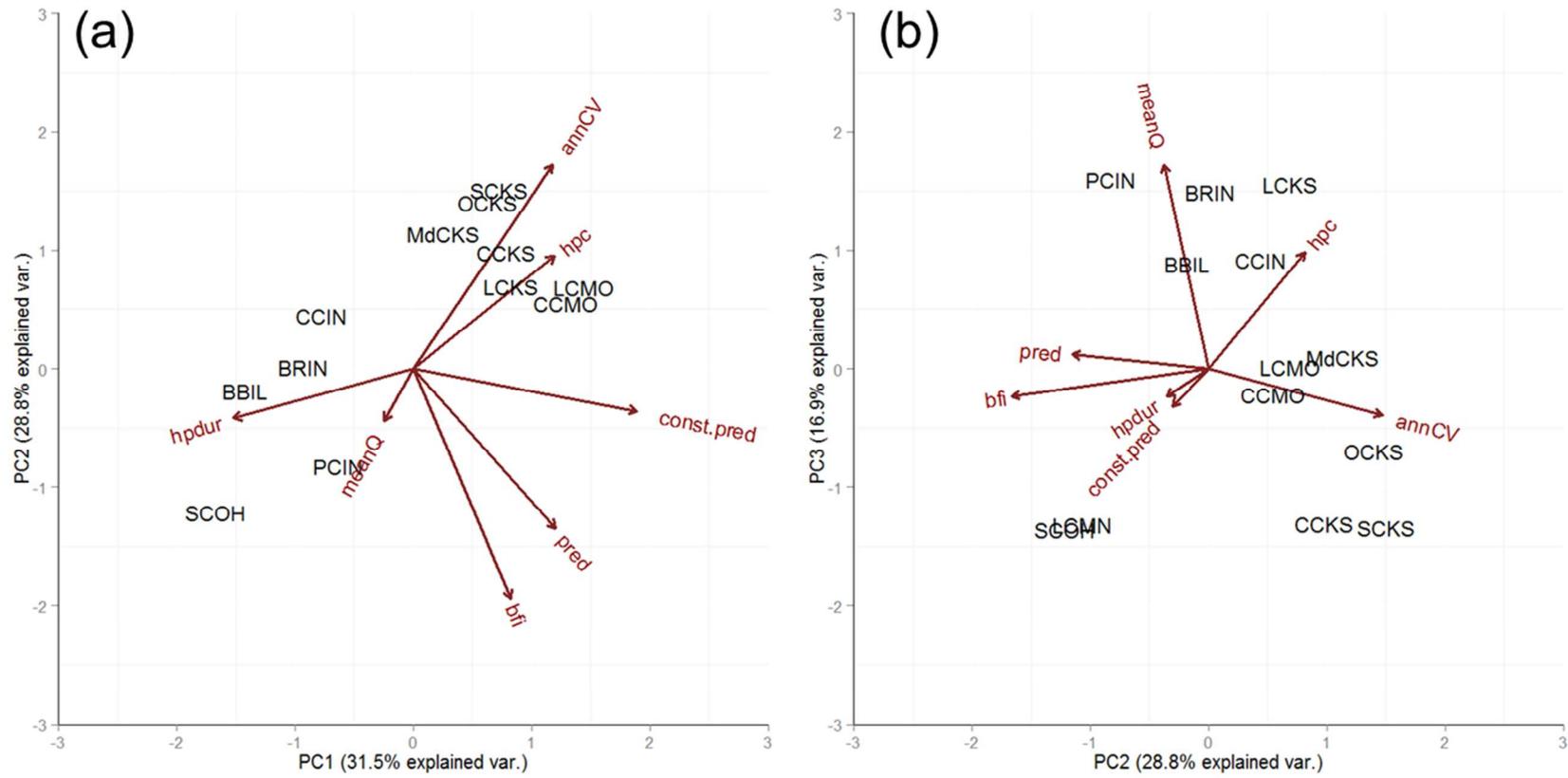


Figure 3. Flow PCAs for Bluntnose Minnow. (a) Flow PC1 (x axis) versus flow PC2 (y axis); (b) Flow PC2 (x axis) versus flow PC3 (y axis). Black text shows site scores. Red arrows and text highlight flow variable vectors.

Appendix S5. Data on life history trait variability among populations.

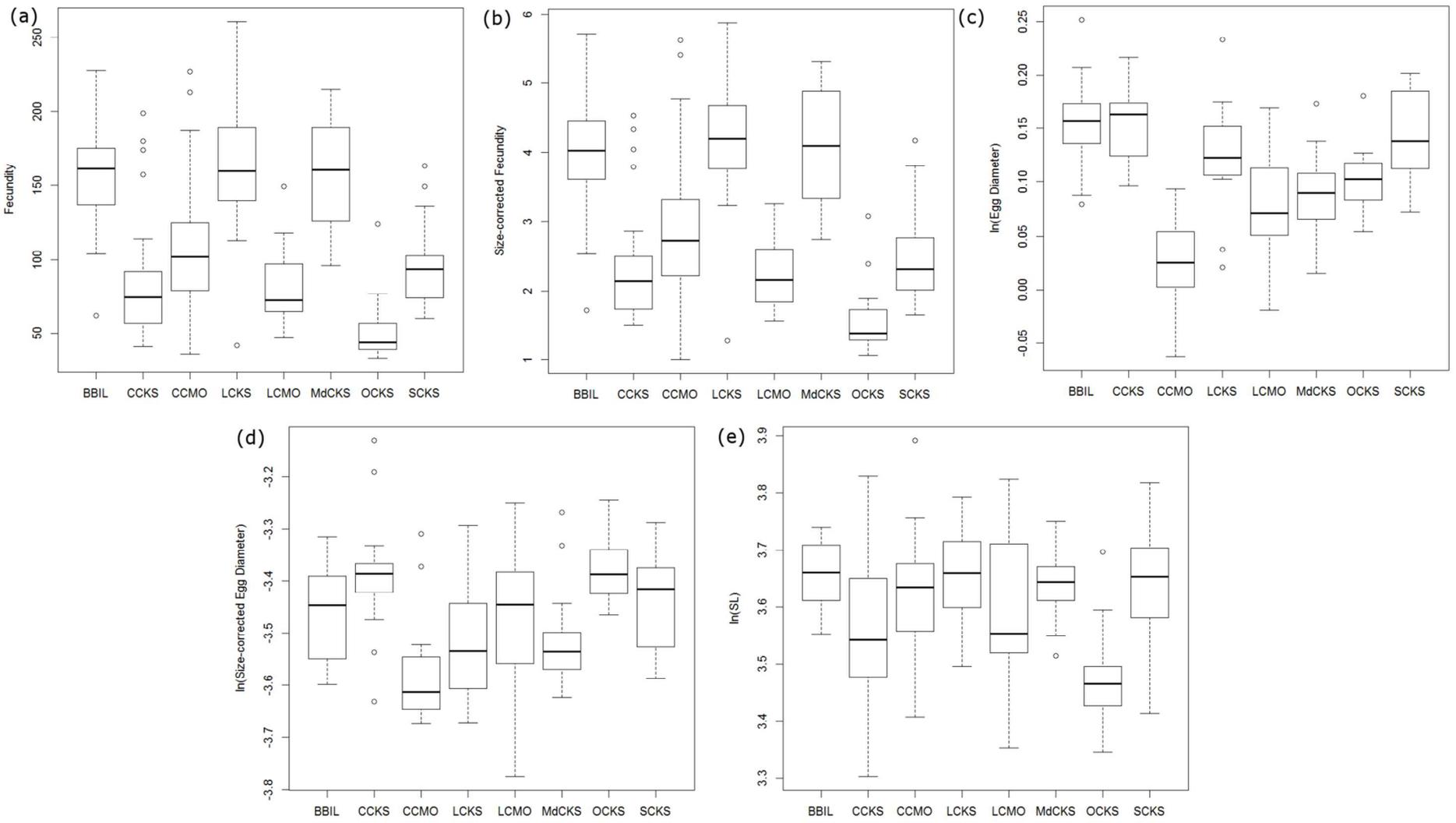


Figure S1. Boxplots showing variation in key traits among populations of orangethroat darter. (a) un-transformed fecundity, (b) size-corrected fecundity, (c) ln-transformed egg size, (d) ln-transformed size-corrected egg size, (e) ln-transformed standard length (SL). Box represents lower and upper quartiles (25% and 75%, respectively) and black line represents median (50% quartile). Whiskers represent 1.5x the box length, with outliers shown.

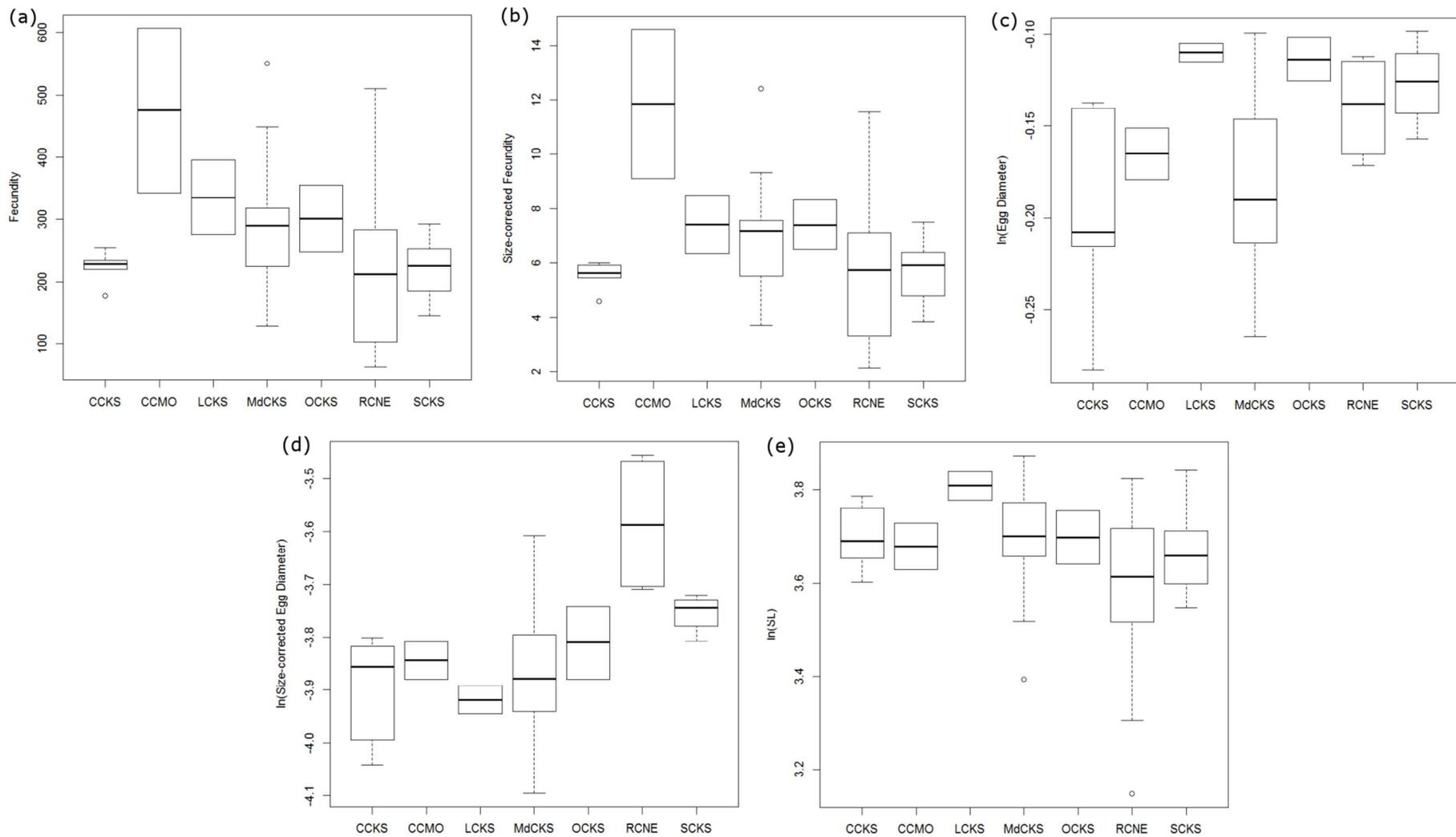


Figure S2. Boxplots showing variation in key traits among populations of red shiner. (a) un-transformed fecundity, (b) size-corrected fecundity, (c) ln-transformed egg size, (d) ln-transformed size-corrected egg size, (d) ln-transformed standard length (SL). Box represents lower and upper quartiles (25% and 75%, respectively) and black line represents median (50% quartile). Whiskers represent 1.5x the box length, with outliers shown.

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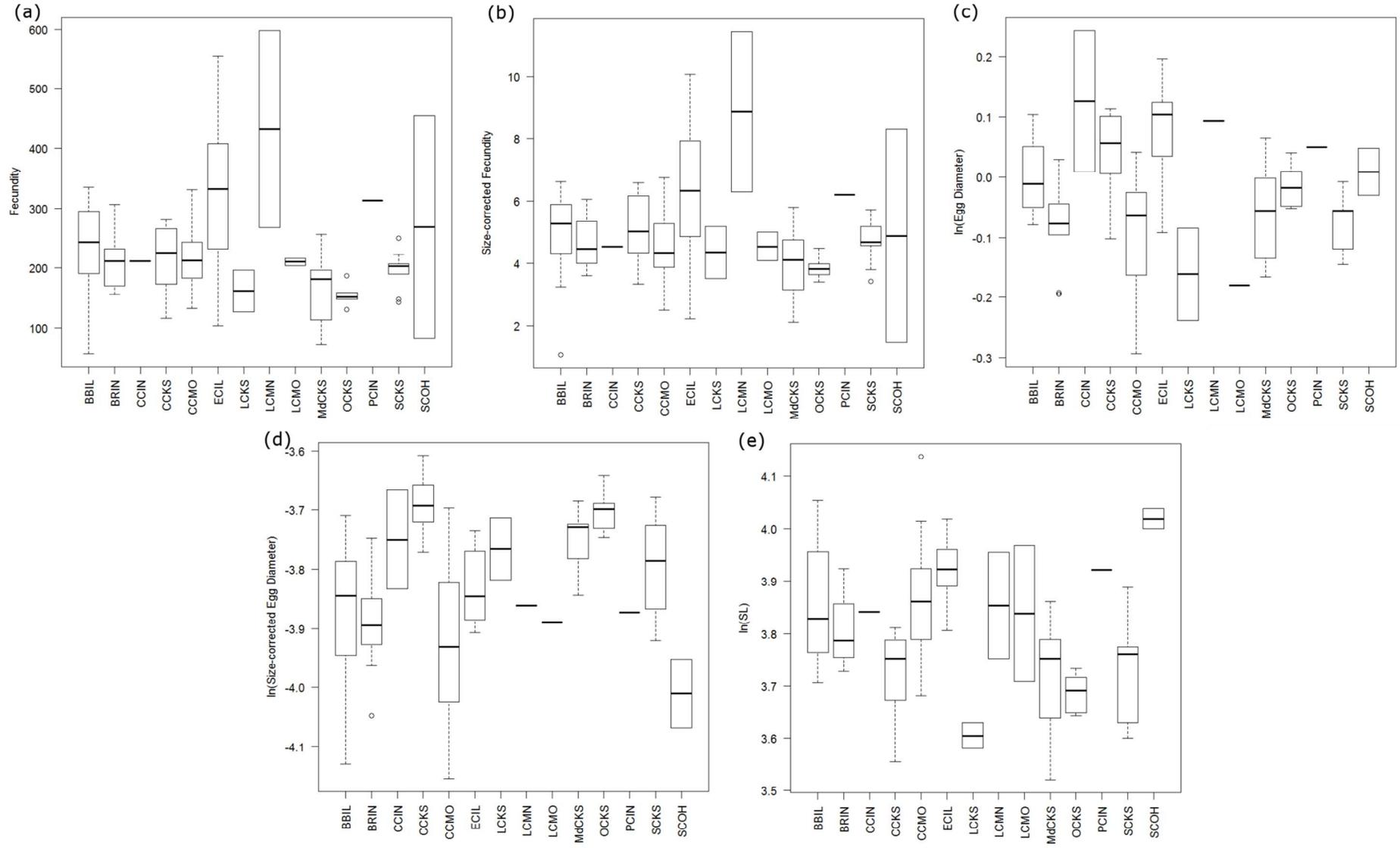


Figure S3. Boxplots showing variation in key traits among populations of bluntnose minnow. (a) un-transformed fecundity, (b) size-corrected fecundity, (c) ln-transformed egg size, (d) ln-transformed size-corrected egg size, (d) ln-transformed standard length (SL). Box represents lower and

1 upper quartiles (25% and 75%, respectively) and black line represents median (50% quartile). Whiskers represent 1.5x the box length, with outliers
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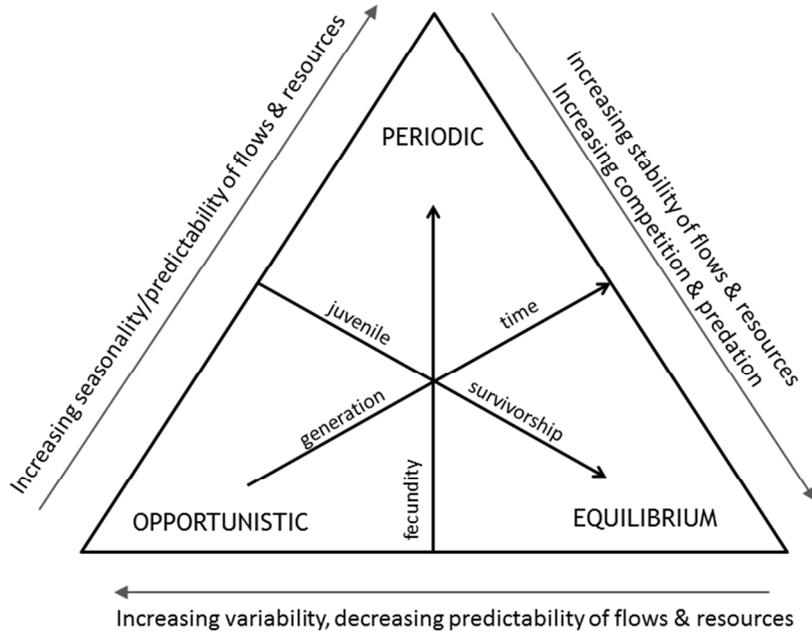
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Appendix S6. Comparison of slopes of linear trait-environment regressions for full datasets (data from all sites for each species included) and for datasets in which sites with small sample sizes (<4 individuals available for estimating trait values for that population) were excluded. Variables from the top ranked models (within $\Delta AICc=2$ of lowest $AICc$) and were selected for comparison of full datasets to those with small sample size sites removed. Slopes of relationships were consistent in direction and generally similar in magnitude compared to results from the full dataset except for a positive relationship between flow PC1 (negative: seasonality) and fecundity in bluntnose minnow in the dataset with small samples removed.

Species	Life history trait	Environmental variable	Slope:	Slope:
			Full dataset	Small removed
Red shiner	Fecundity	Flow PC2	-0.14	-0.05
	Egg size	Flow PC1	+0.05	+0.04
		Latitude	+0.08	+0.11
	MinSLmat	Flow PC1	-0.05	-0.04
Bluntnose minnow	Fecundity	Flow PC1	-0.09	+0.05
		Flow PC2	-0.14	-0.10
		Latitude	+0.12	+0.10
	Egg size	Flow PC2	+0.02	+0.02
		Latitude	-0.02	-0.04
	MinSLmat	Flow PC3	+0.03	+0.02

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Modified from Winemiller 2005, Mims & Olden 2012

Figure 1. The trilateral life history framework of Winemiller and Rose (1992). Modified from Winemiller (2005) and Mims and Olden (2012).
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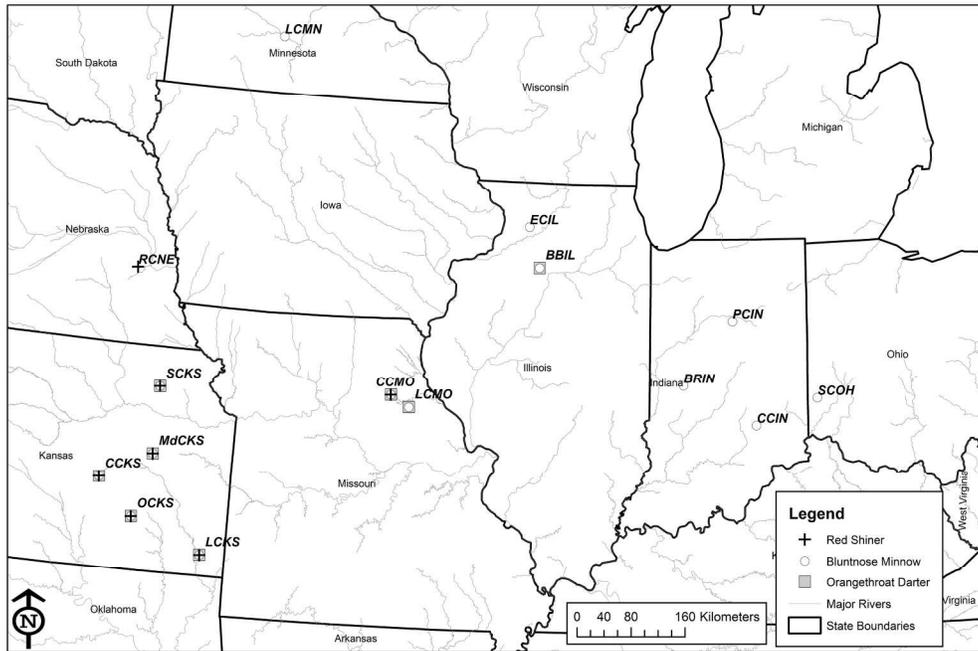


Figure 2. Map of study sites where mature (mature, ripening, or ripe) specimens of target species were found. For site codes and information, see Appendix S1.
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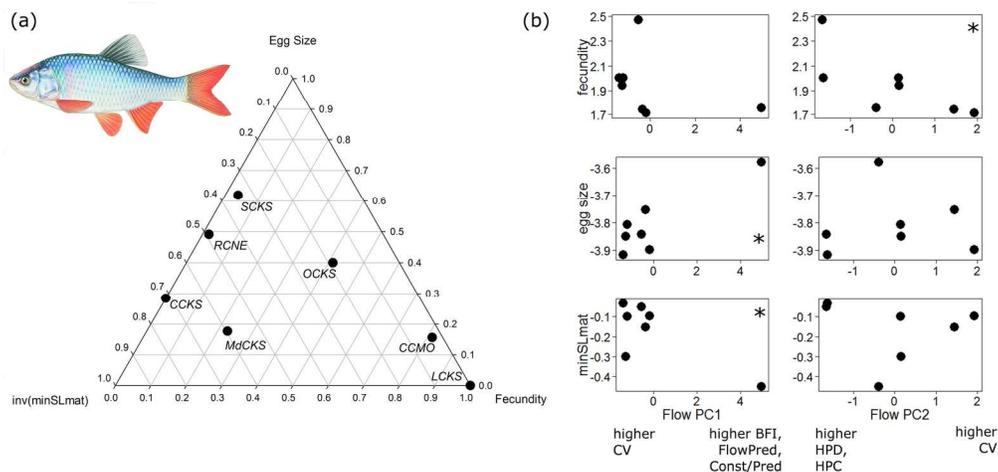


Figure 3. Population life history strategies and flow-trait relationships for red shiner. (a) Ternary plot illustrating trade-offs in traits among populations. Axes scaled between 0 and 1 for the three traits (bottom axis: fecundity; right axis: egg size; left axis: inverse(minSLmat)). Solid circles represent study sites (see Appendix S1). (b) Scatterplots of flow PC-trait relationships. Asterisk indicates important relationship from multiple regression results (Table 2). Higher values of flow PC1 (lower CV), in left panels, were associated with larger eggs and smaller size at maturity. Higher values of flow PC2 (lower HPC, HPD, higher CV), on right panels, were associated with lower fecundity. Illustration of male red shiner copyright and used with permission of Joseph R. Tomelleri.

175x86mm (300 x 300 DPI)

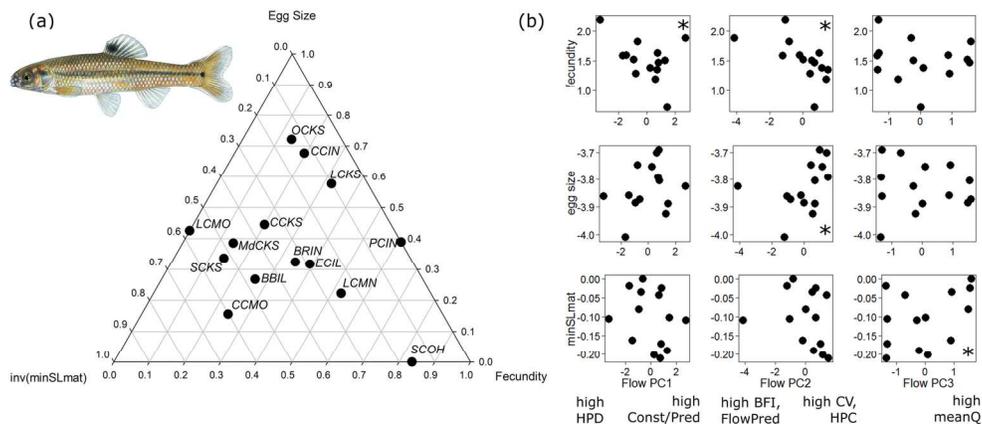


Figure 4. Population life history strategies and flow-trait relationships for bluntnose minnow. (a) Ternary plot illustrating trade-offs in traits among populations. Axes scaled between 0 and 1 for the three traits (bottom axis: fecundity; right axis: egg size; left axis: inverse(minSLmat)). Solid circles represent study sites (see Appendix S1). (b) Scatterplots of flow PC-trait relationships. Asterisk indicates important relationship from multiple regression results (Table 2). Higher values of flow PC1 (lower HPD, higher ConstPred), in left panels, were associated with lower fecundity. Higher values of flow PC2 (higher CV, HPC; lower BFI), in middle panels, were associated with lower fecundity and larger egg size. Higher values of flow PC3 (higher meanQ), right panels, were associated with larger size at maturity. Illustration of male bluntnose minnow copyright and used with permission of Joseph R. Tomelleri.

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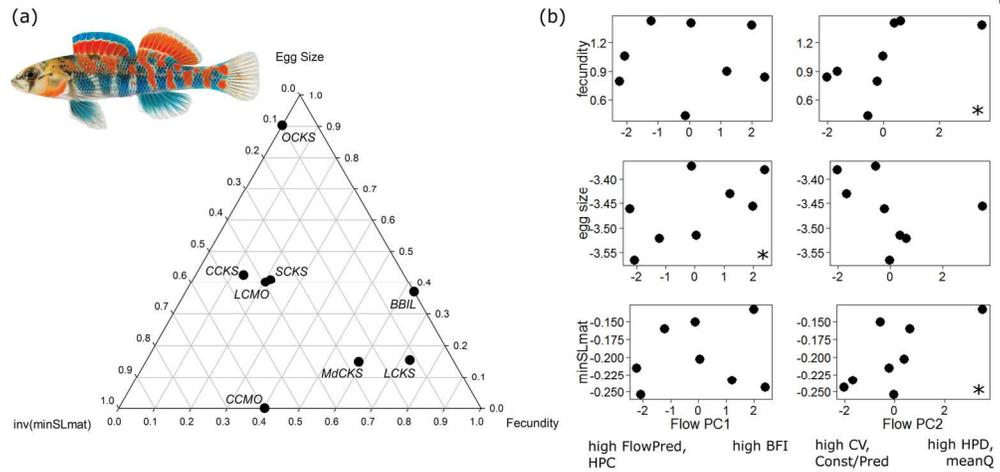


Figure 5. Population life history strategies and flow-trait relationships for orangethroat darter. (a) Ternary plot illustrating trade-offs in traits among populations. Axes scaled between 0 and 1 for the three traits (bottom axis: fecundity; right axis: egg size; left axis: inverse(minSLmat)). Solid circles represent study sites (see Appendix S1). (b) Scatterplots of flow PC-trait relationships. Asterisk indicates important relationship from multiple regression results (Table 2). Higher values of flow PC1 (higher BFI, lower HPC) were associated with larger eggs. Higher values of flow PC2 (higher HPD, lower CV) were associated with higher fecundity and larger size at maturity. Illustration of male orangethroat darter (*E. spectabile pulchellum*) copyright and used with permission of Joseph R. Tomelleri.

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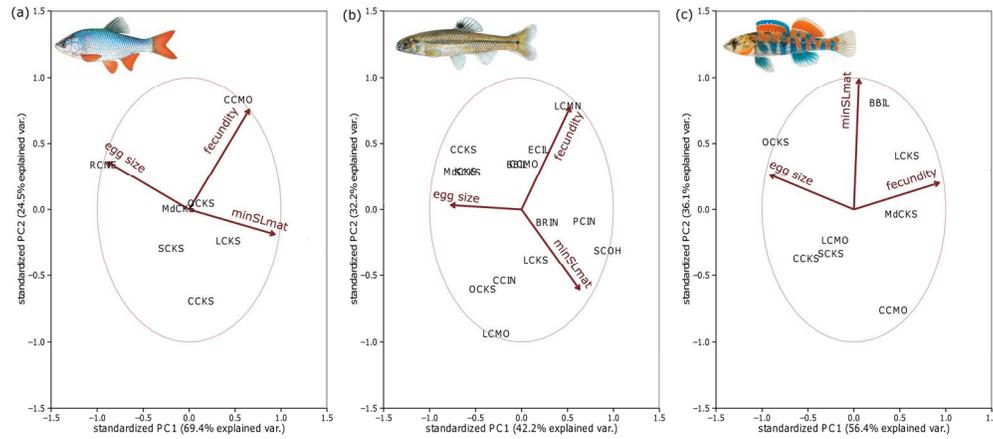


Figure 6. Principal component plots for life history traits for (left to right) red shiner, bluntnose minnow, and orangethroat darter. We interpreted PC1 as an equilibrium (negative) to periodic (positive) axis for all species. We interpreted PC2 as an opportunistic (around zero) to periodic (positive or negative) axis for all species. Red text associated with arrows identifies trait vectors (ln-transformed, size-corrected traits). Uppercase black text identifies site scores (see Appendix S1). Fish illustrations copyright and used with permission of Joseph R. Tomelleri.

177x79mm (300 x 300 DPI)

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