

# Life history theory predicts long-term fish assemblage response to stream impoundment

Joshuah S. Perkin, Natalie E. Knorp, Thomas C. Boersig, Amy E. Gebhard, Lucas A. Hix, and Thomas C. Johnson

**Abstract:** Life history theory predictions for hydrologic filtering of fish assemblages are rarely tested with historical time series data. We retrospectively analyzed flow regime and fish assemblage data from the Sabine River, USA, to test relationships between life history strategies and hydrologic variability altered by impoundment construction. Downstream flow variability, but not magnitude, was altered by completion of Toledo Bend Reservoir (TBR) in 1966. Consistent with life history theory, occurrence of opportunistic strategists declined while equilibrium strategists increased as the fish assemblage was transformed between periods immediately after (1967–1973) and approximately one decade after (1979–1982) completion of TBR. Assemblage transformation was related to decline of opportunistic strategists throughout 250 km of river downstream of TBR. Temporal trajectories for opportunistic and intermediate strategist richness modelled as a function of flow variability converged 12 years postimpoundment. The spatiotemporal scaling of our study is novel among tests of life history theory, and results suggest impoundment-induced alteration to natural hydrologic filtering of fish assemblages can operate on the scale of hundreds of stream kilometres and manifest within approximately one decade.

**Résumé :** Les prédictions découlant de la théorie du cycle biologique concernant le filtrage hydrologique d'assemblages de poissons sont rarement vérifiées à la lumière des données de séries chronologiques passées. Nous avons analysé de manière rétrospective des données sur le régime d'écoulement et l'assemblage de poissons de la rivière Sabine (États-Unis) pour vérifier l'existence de liens entre les stratégies de cycle biologique et la variabilité hydrologique modifiée par la construction d'un ouvrage de retenue. La variabilité des débits en aval, mais non leur magnitude, a été modifiée par l'achèvement du réservoir Toledo Bend (TBR) en 1966. Conformément à la théorie du cycle biologique, la transformation de l'assemblage de poissons entre les périodes suivant immédiatement l'achèvement du TBR (1967–1973) et environ une décennie plus tard (1979–1982) comprenait une diminution de la présence de stratèges opportunistes, mais une augmentation de celle de stratèges d'équilibre. La transformation de l'assemblage était associée au déclin des stratèges opportunistes sur 250 km de la rivière en aval du TBR. Les trajectoires temporelles pour la richesse des stratèges opportunistes et intermédiaires modélisées en fonction de la variabilité des débits convergent 12 ans après la construction de l'ouvrage. L'échelle spatiotemporelle de l'étude se démarque d'autres tests de la théorie du cycle biologique et les résultats donnent à penser que les modifications du filtrage hydrologique naturel des assemblages de poissons induites par les ouvrages de retenue peuvent s'opérer à l'échelle de centaines de kilomètres de cours d'eau en environ une décennie. [Traduit par la Rédaction]

## Introduction

Freshwater ecosystems are threatened by anthropogenic alterations to natural environmental gradients (Malmqvist and Rundle 2002). In lotic ecosystems, global hydrologic gradients are fragmented by >16.7 million impoundments that modify flow regimes, degrade habitats, facilitate species invasions, contribute to population overexploitation, and affect water quality (Poff et al. 1997; Dudgeon et al. 2006; Lehner et al. 2011). The effects of these impoundments on stream flow regimes are likely to worsen under expected global climatic shifts and continued human population growth (Rahel and Olden 2008; Strayer and Dudgeon 2010). Consequently, predictive models capable of relating changes in stream flow to the imperilment of organisms are necessary to inform conservation actions now and in the future (Cooke et al. 2012). Recent advances in predicting organism responses to altered stream flows have hinged on linking ecological traits of organisms to environmental gradients (Arthington et al. 2006;

Olden et al. 2006), including linkages between hydrologic regimes and life history traits (Poff et al. 2006; Mims and Olden 2012; McManamay and Frimpong 2015).

A growing body of theoretical and empirical research suggests stream fish assemblages are structured by interactions between flow regime and fish life history traits (Power et al. 1995; Poff et al. 1997; Lytle and Poff 2004). Life history theory posits that populations are regulated by trade-offs along demographic axes of age at maturity, juvenile survival, and fecundity (Stearns 1977). Because allocation of energy toward growth, survival, and reproduction requires trade-offs along these demographic axes, organisms with unique life history trait combinations experience differential survival across environmental gradients (i.e., environmental filtering; Partridge and Harvey 1988). In the context of fishes, life history traits typically include body size, size and age at maturity, life span, fecundity, ova size, and measures of parental care (Mims et al. 2010). Winemiller and Rose (1992) assembled life history trait data for 216 North American fishes and found that trade-offs ex-

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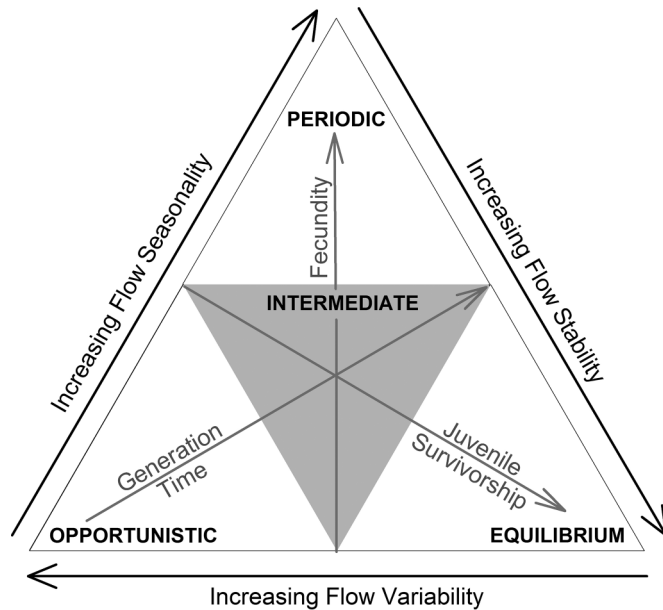
J.S. Perkin, T.C. Boersig, A.E. Gebhard, L.A. Hix, and T.C. Johnson. Department of Biology, 1100 N. Dixie Avenue, Tennessee Technological University, Cookeville, TN 38505, USA.

N.E. Knorp. School of Environmental Studies, 200 W. 10th Street, Tennessee Technological University, Cookeville, TN 38505, USA.

**Corresponding author:** Joshuah S. Perkin (email: [jperkin@tntech.edu](mailto:jperkin@tntech.edu)).

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**Fig. 1.** Conceptual diagram illustrating life history trait trade-offs along gradients of fecundity, generation time, and juvenile survivorship and resulting in four strategist groups: opportunistic (short generation time, low fecundity, low juvenile survival; lower left inner triangle), periodic (long generation time, high fecundity, low juvenile survival; upper inner triangle), equilibrium (long generation time, low fecundity, high juvenile survival; lower right inner triangle), and intermediate (intermediate values of all traits; center inner gray triangle). Gradients for stream flow factors associated with each strategy are shown outside the large triangle. Drawn after Winemiller and Rose (1992).



isted along three primary axes related to fecundity, juvenile survivorship, and age at maturity. The “trilateral continuum” model described by Winemiller and Rose (1992) provides theoretical expectations for organism responses to environmental variation based on proximity to three end-point life history strategies (Fig. 1). Opportunistic strategists are characterized by young age at maturation, low fecundity, and low juvenile survival, and fishes employing this life history strategy are expected to inhabit highly variable environments in which rapid recolonization and population growth are necessary for persistence. Periodic strategists are characterized by old age at maturation, high fecundity, and low juvenile survival, and fishes employing this strategy are expected to inhabit environments characterized by cyclic fluctuations. Equilibrium strategists are characterized by old age at maturation, low fecundity, and high juvenile survival, and fishes employing this strategy are expected to inhabit stable environments in which biotic interactions outweigh the effects of environmental interactions. Within multivariate trait space between these three end points, there exists a continuum of intermediate fish life history trait combinations (Winemiller 2005).

Since the inception of the trilateral continuum model, empirical evidence from fish assemblages has linked theoretical expectations to observed patterns on a global scale. For example, Tedesco et al. (2008) found higher abundances of periodic strategists in western Africa streams characterized by seasonal shifts in flow, but equilibrium strategists were dominant in streams with stable hydrologic regimes. Olden and Kennard (2010) assess life history trait convergences along hydrologic gradients for North American and Australian fishes and found support for the trilateral continuum model across continents, despite large phylogenetic and historical differences among assemblages. More recently, Mims and Olden (2012) reviewed fish assemblage data from 109 sites in

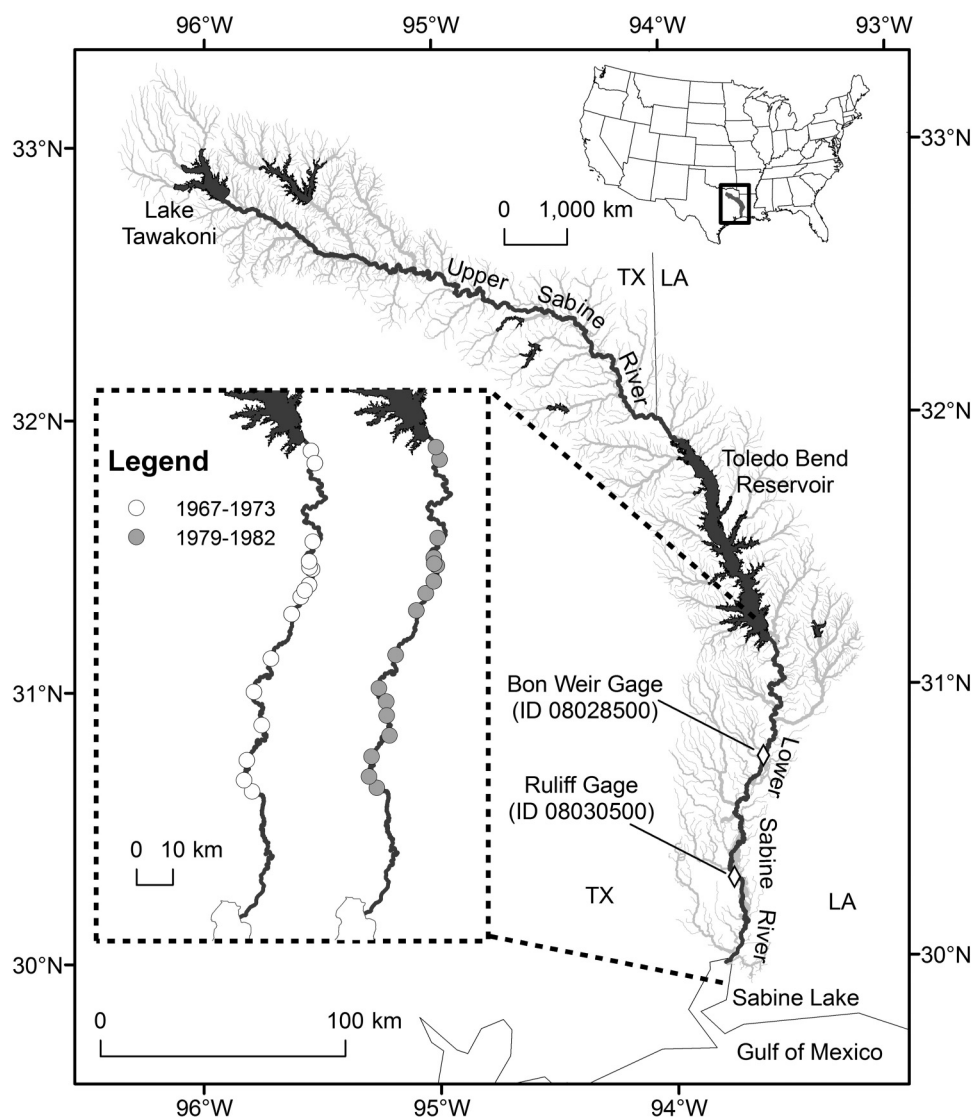
the USA and found positive correlations between flow variability and opportunistic strategists, flow seasonality and periodic strategists, and flow stability and equilibrium strategists. Collectively, these and other studies support life history theory as a framework for predicting fish–flow relationships across gradients of hydrologic regimes, in part because traits are filtered on evolutionary time scales (e.g., centuries to millennia) to shape species adaptations and occurrences (Heino et al. 2013; Bergerot et al. 2015; Meador and Brown 2015). However, relatively few studies have addressed the extent to which changes in hydrologic regimes caused by impoundment construction and flow alteration might filter fish species occurrence on ecological time scales (e.g., decades to centuries).

To date, application of life history theory has focused on spatially discrete basins with contrasting flow regimes without regard for long-term, temporal flow variability within basins (Czeglédi and Ers 2013). Therefore, applying life history theory to predict fish responses to impoundment construction or operation represents a major research need, because impoundment numbers are expected to continue to expand on a global scale (Lehner et al. 2011; Olden 2016). Existing studies suggest long-term shifts in fish assemblage structure in the Colorado River Basin, USA, were at least partly related to modified flows differentially filtering life history traits, but separating pure flow regime effects from those caused by a large number of non-native species is difficult (Olden et al. 2006; Pool et al. 2010; Gido et al. 2013). Similarly, comparisons of fish communities at dam-influenced sites and distant reference sites highlight assemblage differences that are consistent with life history theory (Mims and Olden 2013), but such frameworks do not directly test temporal shifts experienced by assemblages sampled at the same sites over time. Consequently, there is a need to examine relationships between environmental alteration and ecological responses at spatiotemporal scales at which critical fish life history events operate, including stream segments ( $10^5$  m) afflicted by riverscape alteration (Fausch et al. 2002). Here, we used historical fish collections from the Sabine River in the southeastern USA to test life history theory expectations regarding assemblage change caused by impoundment construction. Our objectives included (i) testing for downstream change in flow regime caused by impoundment construction; (ii) testing for downstream change in assemblage structure, including species’ life history strategies based on “soft” (i.e., a continuum between end points) and “hard” (i.e., single end-point assignment) classifications; and (iii) testing for a relationship between flow regime change and fish assemblage change. Because opportunistic strategists dominate stream fish assemblages in the southeastern USA (Mims et al. 2010) and based on current life history theory, we predicted reduced flow variability caused by impoundment construction would negatively affect opportunistic, not influence periodic or intermediate, and positively affect equilibrium strategist occurrences (Mims and Olden 2013).

### Study area

The Sabine River drains 25 270 km<sup>2</sup> as it flows southeast along the border of Texas and Louisiana, USA, to Sabine Lake, an embayment to the Gulf of Mexico. Major land cover types include forest (67% cover), grassland (15%), agriculture (10%), and urbanization (8%), and human population density ranges from <6 people·km<sup>-2</sup> in rural areas to >160 people·km<sup>-2</sup> in urbanized areas (Dahm et al. 2005). Toledo Bend Reservoir (TBR) impounds 160 km of the mainstem Sabine River and separates the upper and lower Sabine River basins (Fig. 2). The surface area of TBR is 749 km<sup>2</sup>, making it the largest reservoir in the Sabine River basin and the fifth largest in the USA. Construction of the 34 m tall Toledo Bend Dam began in 1964, was completed in 1966, and the reservoir finished filling in 1968 (Suttkus and Mettee 2009). Construction of TBR isolated at least 250 river km of freshwater fish habitat between approximately Burkeville, Texas, and Sabine Lake, and 80 km of this

**Fig. 2.** Distribution of fish assemblage samples collected from the Sabine River, USA, downstream of Toledo Bend Reservoir during Period 1 (open circles, 1967–1973) and Period 2 (grey circles, 1979–1982), and the locations of US Geological Survey gages.



isolated fragment of stream is considered a Scenic River (Dahm et al. 2005). Fish habitats in the lower Sabine River downstream of TBR include low-gradient slopes, active lateral channel migration with high flood plain connectivity, sandy substrates (<2 mm diameter), and shifting sand bars with a maximum main channel depth of 3 m and mean width of 100 m (Phillips 2008).

## Methods

### Flow regime alteration

We downloaded daily flow data from two US Geological Survey (USGS) gages downstream of TBR, the first near Bon Weir, Texas (USGS No. 08028500; ~80 river km downstream of TBR) and the second near Ruliff, Texas (USGS No. 08030500; ~175 river km downstream of TBR). Daily flow data were downloaded from each gage for the period 1927–2007, so that 40 years of pre-impoundment and 40 years of postimpoundment data were used for each gage. We used indicators of hydrologic alteration (IHA; Richter et al. 1996) to summarize annual flows prior to (1927–1966) and following (1967–2007) completion of TBR using 34 commonly applied stream flow metrics (Mathews and Richter 2007). All metrics were calculated using a water year defined as 1 October through 30 September (Table 1). We summarized latent hy-

drologic gradients composed of linear combinations of flow metrics using principal component analysis (PCA) from the “rda” function in the “vegan” package in Program R (Oksanen et al. 2016). Principal components (PCs) were retained for interpretation based on broken stick models (Jackson 1993), and we illustrated temporal trends in flow gradients by plotting annual scores from the retained PCs. We tested for significant changes in flow gradients for the period 1967–1982 (same period as fish assemblage data; see below) using a generalized least squares (GLS) model with an autocorrelation function in which time was the predictor variable and PC scores were the response variable. We used the “gls” function from the “nlme” package in Program R to model the relationship between flows and time. We repeated this process for the Bon Weir and Ruliff gages to assess the spatial effect of TBR on lower Sabine River flows.

### Fish assemblage data

Royal Suttkus (Tulane University; Bart 2010) and colleagues collected fish assemblage samples throughout the southeastern USA between 1950 and 2005. These collections are housed in the Tulane Museum of Natural History (TMNH), and species abundance data associated with collections are compiled online ([www.tubri](http://www.tubri)).



**Table 1.** Indicators of hydrologic alteration flow metrics, codes used in principal component analysis (PCA) plots (see Fig. 3), metric descriptions, and PC scores for flows measured at US Geological Survey gages near Bon Weir, Texas (USGS No. 08028500) and Ruliff, Texas (USGS No. 08030500).

Flow parameter	Code	Description	Bon Weir		Ruliff	
			PC 1	PC 2	PC 1	PC 2
<b>Annual flow variation</b>						
Annual CV	AnnCV	Standard deviation of all yearly flow values/mean annual flow	0.78	1.26	0.70	1.39
<b>Monthly flows</b>						
January	Jan	Median flows for January	-1.37	0.60	-1.46	0.51
February	Feb	Median flows for February	-1.38	1.04	-1.40	1.07
March	Mar	Median flows for March	-1.44	0.98	-1.47	0.90
April	Apr	Median flows for April	-1.24	0.98	-1.31	0.82
May	May	Median flows for May	-0.90	1.31	-0.94	1.14
June	Jun	Median flows for June	-1.18	0.13	-1.13	0.31
July	Jul	Median flows for July	-1.33	-1.10	-1.26	-1.02
August	Aug	Median flows for August	-1.22	-1.38	-1.11	-1.17
September	Sep	Median flows for September	-1.29	-1.17	-1.25	-1.06
October	Oct	Median flows for October	-0.94	-1.19	-0.96	-1.47
November	Nov	Median flows for November	-1.16	-0.58	-1.16	-0.92
December	Dec	Median flows for December	-1.33	0.02	-1.34	-0.32
<b>Flow magnitude</b>						
1-day minimum	1Dmin	Annual minima, 1-day mean	-1.46	-1.52	-1.33	-1.84
3-day minimum	3Dmin	Annual minima, 3-day means	-1.44	-1.64	-1.30	-1.89
7-day minimum	7Dmin	Annual minima, 7-day means	-1.40	-1.69	-1.30	-1.89
30-day minimum	30 min	Annual minima, 30-day means	-1.45	-1.57	-1.37	-1.76
90-day minimum	90 min	Annual minima, 90-day means	-1.65	-0.83	-1.65	-1.03
1-day maximum	1Dmax	Annual maxima, 1-day mean	-1.54	1.28	-1.53	1.21
3-day maximum	3Dmax	Annual maxima, 3-day means	-1.54	1.35	-1.54	1.25
7-day maximum	7Dmax	Annual maxima, 7-day means	-1.56	1.43	-1.57	1.34
30-day maximum	30max	Annual maxima, 30-day means	-1.62	1.35	-1.65	1.33
90-day maximum	90max	Annual maxima, 90-day means	-1.70	1.20	-1.72	1.14
No. of zero days	ZeroD	No. of days with zero flow	0.00	0.00	0.00	0.00
Base flow index	Base	7-day minimum/mean annual flow	0.62	-2.32	0.69	-2.32
<b>Time of flows</b>						
Date of minimum	Datemin	Julian date of annual 1-day minimum	0.07	0.73	-0.01	0.39
Date of maximum	Datemax	Julian date of annual 1-day maximum	0.07	-0.15	-0.05	-0.60
<b>Frequency of flows</b>						
Low pulse count	Lopul#	No. of low flow pulses in a year	0.77	-1.64	1.04	-0.98
Low pulse duration	LopulL	Median duration (days) of low flow pulses	0.72	1.89	0.74	1.87
High pulse count	Hipul#	No. of high flow pulses in a year	-1.23	0.62	-1.13	1.04
High pulse duration	HipulL	Median duration (days) of high flow pulses	-0.88	1.35	-1.13	0.72
<b>Rate of change in flows</b>						
Rise rate	Riserate	Median of all positive differences between consecutive daily flows	-1.64	-0.20	-1.55	0.50
Fall rate	Fallrate	Median of all negative differences between consecutive daily flows	-1.71	-0.61	-1.79	-0.57
No. of reversals	Reversals	No. of hydrologic reversals	-0.29	-2.19	0.10	-2.03

org/suttkus/fieldnotes.aspx). In the lower Sabine River, collections were conducted using a seine (3.05 m by 1.83 m) in which all seineable habitats at a site were sampled, captured fishes were sorted and identified to species, and specimens were catalogued and deposited in the TMNH (see details in Suttikus and Mettee 2009). We were unable to include measurements of effort (e.g., area sampled, number of seine hauls) at each site because stored field notes were destroyed by a hurricane prior to electronic backup (see Suttikus and Mettee 2009). To address this data limitation, we only used occurrence data (i.e., presence-absence) and stress that our analyses are contingent on the assumption that approximately equal effort was afforded through space and time. We believe this assumption to be reasonable because the same individual was responsible for all collections, the same sampling gear was used, and these and other data collected by Royal Suttikus are routinely used to quantify historical changes in fish assemblages in the southeastern USA (Onorato et al. 2000; Suttikus and Mettee 2009; Geheber and Piller 2012). Available collection data included 149 collections (i.e., a collection includes all fishes collected at a single site on a single date) taken during the years between 1967 and 1982. Time intervals were unequal and included 1967 (2 collections), 1968 (8), 1969 (29), 1970 (51), 1971 (7), 1972 (1),

1973 (2), 1979 (21), 1980 (7), and 1982 (21). The months during which collections were made included January (10 collections), February (18), March (3), April (3), May (17), July (49), August (21), October (8), and November (20). At the broadest scale, we identified two periods during which collections could be combined, including collections made shortly after impoundment (Period 1; 1967–1973) and collections made approximately one decade after impoundment (Period 2; 1979–1982). When combined at this scale, collections during Periods 1 and 2 spanned a similar extent of the lower Sabine River (Fig. 2 inset). In total, 42 species occurred in at least 5% of the 149 collections (Table 2), and all of these species are considered native to the lower Sabine River (Hubbs et al. 2008).

### Reproductive trait data

We used existing life history trait databases to classify fishes according to their life history strategy. We primarily relied on the database described in Mims et al. (2010), but we supplemented this database with classifications from Hoenig et al. (2007) when Sabine River species were absent. Strategy classifications from Mims et al. (2010) represented “soft” classifications based on ordination results along three axes, including  $\ln(\text{fecundity})$ ,  $\ln(\text{length at maturation})$ , and  $\ln(\text{egg size} + 1) + \ln(\text{parental care} + 1)$ . Fecundity

**Table 2.** Species, codes, NMDS axes 1 and 2 scores (see Fig. 4), strategy weight for opportunistic (Opp), periodic (Per), and equilibrium (Equ) strategist endpoints (from Mims and Olden 2012; see text), and hard classification (H-Class, including intermediate classifications = Inter; see Fig. 1) for 42 fishes collected from the Sabine River, USA, during 1967–1982.

Species	Code	NMDS1	NMDS2	Opp	Per	Equ	H-Class
<i>Ammocrypta clara</i>	Acla	-0.052	0.247	0.876	0.294	0.176	Opp
<i>Ammocrypta vivax</i>	Aviv	0.077	0.184	0.876	0.294	0.176	Opp
<i>Aphredoderus sayanus</i>	Asay	-0.186	-0.882	0.635	0.179	0.348	Opp
<i>Carpionides carpio</i>	Ccar	-0.138	0.478	0.421	0.829	0.324	Per
<i>Cyprinella lutrensis</i>	Clut	-0.417	0.111	0.663	0.324	0.362	Opp
<i>Cyprinella venusta</i>	Cven	0.049	0.178	0.706	0.260	0.319	Opp
<i>Dorosoma cepedianum</i>	Dcep	0.212	-0.135	0.406	0.839	0.187	Per
<i>Dorosoma petenense</i>	Dpet	-0.012	0.102	0.658	0.628	0.185	Inter
<i>Etheostoma chlorosoma</i>	Echl	-0.284	-0.724	0.744	0.254	0.286	Opp
<i>Etheostoma gracile</i>	Egra	-0.577	-0.386	0.764	0.363	0.230	Opp
<i>Fundulus notatus</i>	Fnot	0.053	-0.344	0.805	0.275	0.284	Inter
<i>Fundulus olivaceus</i>	Foli	0.003	-0.313	0.788	0.262	0.268	Inter
<i>Gambusia affinis</i>	Gaff	-0.029	-0.061	—	—	—	Inter
<i>Hybognathus nuchalis</i>	Hnuc	-0.225	0.069	0.738	0.554	0.177	Opp
<i>Hybopsis amnis</i>	Hamm	-0.296	-0.635	0.708	0.460	0.270	Opp
<i>Ictalurus punctatus</i>	Ipun	-0.313	-0.459	0.148	0.377	0.765	Equ
<i>Labidesthes sicculus</i>	Lsic	-0.063	-0.041	—	—	—	Inter
<i>Lepomis gulosus</i>	Lgul	-0.273	-0.812	0.426	0.481	0.467	Inter
<i>Lepomis humilis</i>	Lhum	-0.212	-0.790	0.630	0.387	0.373	Opp
<i>Lepomis macrochirus</i>	Lmac	0.457	-0.278	0.379	0.490	0.520	Inter
<i>Lepomis megalotis</i>	Lmeg	0.110	-0.079	0.473	0.428	0.480	Inter
<i>Lepomis microlophus</i>	Lmic	0.890	-0.083	0.342	0.513	0.578	Inter
<i>Lythrurus fumeus</i>	Lfum	-0.439	-0.445	0.826	0.329	0.193	Opp
<i>Macrhybopsis hyostoma</i>	Mhyo	-0.546	-0.402	0.769	0.519	0.186	Opp
<i>Menidia beryllina</i>	Mber	1.066	0.129	—	—	—	Inter
<i>Micropterus punctulatus</i>	Mpun	0.292	0.011	0.346	0.556	0.657	Inter
<i>Micropterus salmoides</i>	Msal	0.470	-0.144	0.296	0.541	0.647	Inter
<i>Minytrema melanops</i>	Mmel	0.015	-0.863	0.432	0.709	0.473	Per
<i>Moxostoma poecilurum</i>	Mpoe	-0.209	-0.717	0.360	0.629	0.652	Inter
<i>Notemigonus crysoleucas</i>	Ncry	-0.272	-0.420	0.559	0.624	0.101	Inter
<i>Notropis atherinoides</i>	Nath	-0.452	-0.319	0.757	0.523	0.136	Opp
<i>Notropis buchanani</i>	Nbuc	-0.492	-0.348	0.836	0.411	0.163	Opp
<i>Notropis sabinae</i>	Nsab	0.076	0.185	0.836	0.411	0.163	Opp
<i>Notropis texanus</i>	Ntex	-0.151	-0.253	0.836	0.411	0.163	Opp
<i>Notropis volucellus</i>	Nvol	-0.119	0.020	0.946	0.347	0.067	Opp
<i>Noturus nocturnus</i>	Nnoc	0.051	-0.670	0.526	0.185	0.502	Inter
<i>Opsopoeodus emiliae</i>	Oemi	-0.210	-0.432	0.690	0.283	0.369	Opp
<i>Percina sciera</i>	Psci	-0.078	-0.330	0.702	0.374	0.339	Opp
<i>Phenacobius mirabilis</i>	Pmir	0.153	-0.431	0.708	0.460	0.270	Opp
<i>Pimephales vigilax</i>	Pvig	-0.144	0.088	0.669	0.330	0.374	Opp
<i>Pomoxis annularis</i>	Pann	-0.217	-0.599	0.327	0.589	0.480	Inter
<i>Pomoxis nigromaculatus</i>	Pnig	-0.177	-0.573	0.345	0.568	0.512	Inter

was defined as the number of eggs per female per spawning season, length of maturation was defined as the mean size (total length, TL) of females at maturation, egg size was defined as the mean diameter of fully developed ovarian oocytes, and parental care was defined according to the methods described by Winemiller (1989). The relative affinity of each species to each strategy end point was calculated following the methods of Mims and Olden (2012). Briefly, this included calculating the Euclidean distance in trivariate life history space (i.e., within the trilateral continuum model) between each species location and each of three life history strategy end points (opportunistic, periodic, and equilibrium). These distances were then normalized between 0 and 1, and the inverse was computed to yield a “strategy weight” along each life history gradient so that three values were calculated for each species (see Olden and Kennard 2010). Classifications of species by Hoinghaus et al. (2007) followed a similar ordination approach, but “hard” classifications (i.e., a single end-point value assigned) were reported, including a fourth category for species without proximity to any end point (i.e., “intermediate” strategists). We addressed discrepancies between the two life history trait classi-

fication schemes by including hard classifications for all species collected from the lower Sabine River. For the first database, single end-point strategies (i.e., opportunistic, periodic, or equilibrium) were assigned to species with strategy weights > 0.60 for a single strategy, and species with strategy weights < 0.60 for all end points were assigned to the intermediate category. When discrepancies in hard classifications occurred between Mims et al. (2010) and Hoinghaus et al. (2007), the species in question were assigned to the intermediate strategy group (Table 2). We then employed a combination of analyses that focused on soft and hard classifications to test life history theory predictions.

#### Statistical analyses

We retained all species that occurred in >5% of collections (i.e., at least 8 of 149) to address any disproportional statistical influences by rare species (Jackson et al. 1989; Anderson and Willis 2003). We first used nonmetric multidimensional scaling (NMDS) to illustrate the two-dimensional distribution of pairwise Bray-Curtis distances between samples and applied analysis of similarity (ANOSIM) to test for change between the two periods. We used

the “metaMDS” function from the “vegan” Package in Program R to run the NMDS and ANOSIM. We also extracted species scores that represented the weighted sums from the assemblage matrix to determine which species occurred most in collections taken during each time period (Borcard et al. 2011). We compared the distribution of species scores along NMDS 1 with life history strategy weights (i.e., soft classifications) to test for changes in species strategies between periods. Species without soft classifications were excluded from regression analysis. Because relationships violated assumptions of ordinary least squares regression (i.e., normality, standardized variances, and linear relationship), we used a generalized additive model (GAM) with a beta regression error term (i.e., for bound (0,1) data) to test for significance of smoothing terms (Zuur et al. 2007). Given the exploratory nature of our analysis, we fit regression models for each life history end-point strategy and assessed significance at  $\alpha = 0.05$  rather than adjust the significance level to accommodate multiple tests (Gido et al. 2013).

Stream fish assemblage responses to impoundments can attenuate with distance away from the dam if flow effects are “diluted” by tributary inflows (Kinsolving and Bain 1993). To account for this effect, we assessed spatial autocorrelation in assemblage change between periods with increasing downstream distance from TBR using hard classifications. Because hard classifications predominantly included opportunistic and intermediate strategists, we excluded periodic and equilibrium strategists from this analysis. Furthermore, because our interest was in assemblage change at the temporal resolution of periods, it was necessary to control for seasonal effects caused by collections made during different months or annual effects caused by samples taken during different years. We used a generalized additive mixed modelling (GAMM) approach in which the number of strategists (i.e., number of taxonomically unique strategists) in a collection was the response variable, distance downstream of TBR was a fixed variable with a fitted smoothing term, period was a fixed factor, month and year were included as random variables, a Poisson error distribution was used, and an autocorrelation function (i.e., AR1) was included to account for nonindependence among samples taken close together in space (measured using kilometres downstream of dam). We fit GAMMs using a hierarchical modeling framework in which we first included period as a factor, and if significant, GAMMs were then fit for each period individually. This approach allowed for a “global” test of the effect of period and then a period-specific effect of longitudinal distance downstream from TBR (Zuur et al. 2014). We used the “gamm” function from the “mgcv” package in Program R to fit GAMMs for opportunistic and intermediate strategists independently and assessed significance at  $\alpha = 0.05$ .

Our final objective was to assess the relationship between change in flow regime and change in life history strategist occurrence. Current life history theory suggests reductions in flow variability should negatively correlate with opportunistic strategist occurrence (Mims and Olden 2012, 2013). Because flow regime gradient analysis indicated PC 2 was associated with a decline in flow variability through time (see Results), we used the fitted GLS function between time and PC 2 to predict strategist richness for hard classifications of opportunistic and intermediate strategists. Fits of the PC 2 function from the Bon Weir and Ruliff gages produced similar results, so we only show the Bon Weir gage data here because it was the gage closest to the center of the study area. Because relationships were nonlinear and violated assumptions of normality and standardized variances, we fit GAMMs with the PC 2 flow function as a fixed variable with a smoothing function, included month and year as random variables, and used a quasi-Poisson error term with an overdispersion parameter to account for samples with relatively extreme richness values with high leverage. We illustrated the flow–richness relationships along the PC 2 flow function gradient as well as the temporal sequence of fits to illustrate the change in opportunistic and intermediate

strategists through time. All analyses were conducted in Program R version 3.1.3 (R Core Team 2015).

## Results

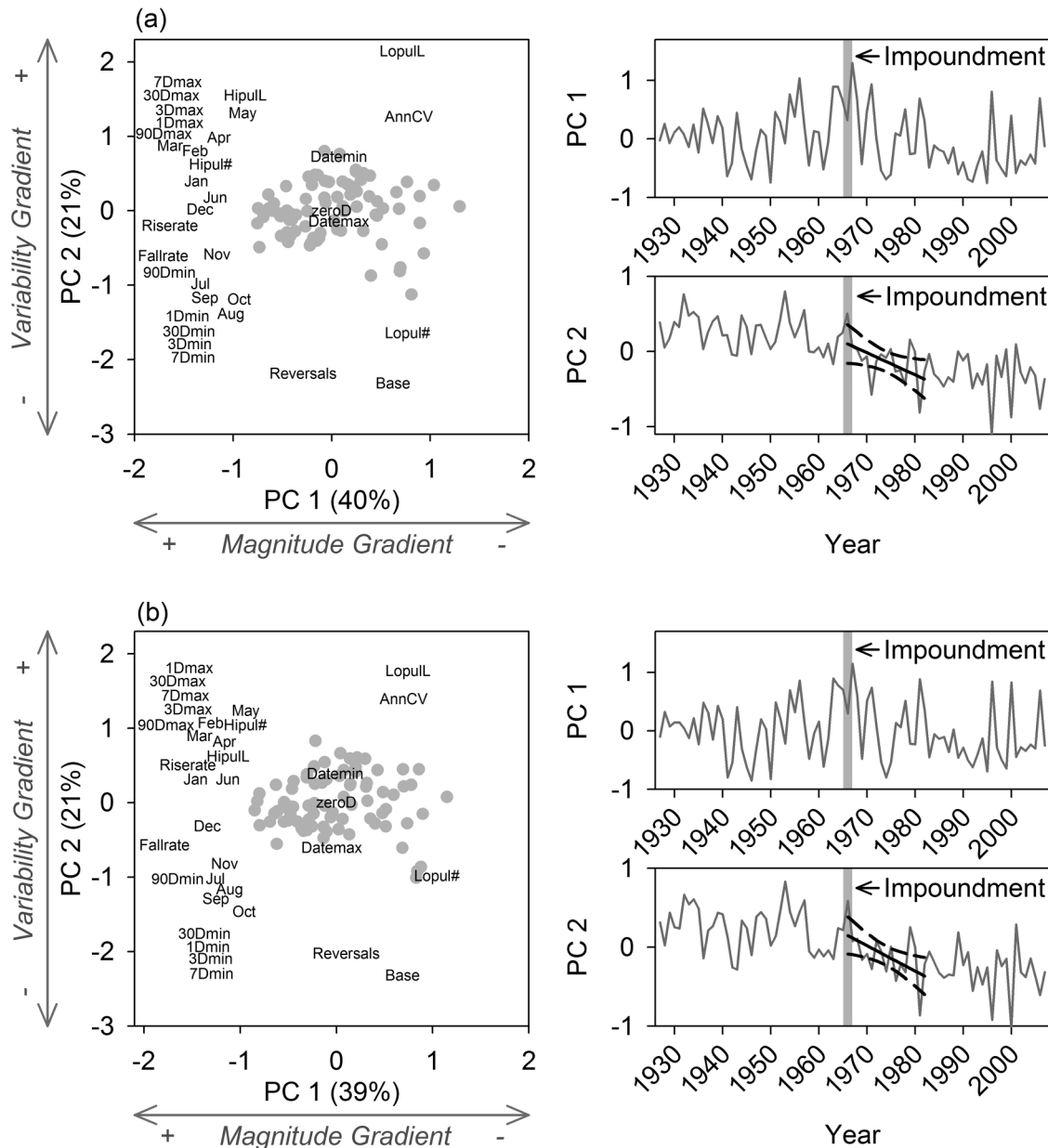
Flow gradients summarizing 34 flow variables were consistent between the Bon Weir and Ruliff gages (Table 1). Broken stick models suggested the first two PCs at each gage should be retained for interpretation. At the Bon Weir gage, PC 1 described 40% of variation in flow metrics and represented a gradient in discharge magnitude (Fig. 3a). All monthly flow magnitudes, all maximum flow magnitudes, and all minimum flow magnitudes were negatively associated with PC 1, whereas low pulse number, low pulse length, base flow, and annual coefficient of variation (CV) were positively associated with PC 1. The second PC described 21% of variation and represented a gradient in flow variability. All measurements of minimum flow magnitude, base flow, and late-summer – early-fall monthly magnitudes (July, August, September, and October) were negatively associated with PC 2, whereas all measurements of maximum flow magnitude, high pulse length, and annual CV were positively associated with PC 2. Temporal trajectories for PC 1 indicated no significant trend following impoundment (1967–1982;  $t = 0.51$ ,  $P = 0.619$ ); however, the temporal trajectory for PC 2 included significant reduction in flow variability following construction of TBR ( $t = 2.11$ ,  $P < 0.05$ ). At the Ruliff gage, PC 1 described 39% of variation, PC 2 described 21%, flow metrics scores along PCs were consistent with the Bon Weir gage, and temporal trends included no significant change for PC 1 ( $t = 0.29$ ,  $P = 0.772$ ) and a significant decline in flow variability along PC 2 ( $t = 2.52$ ,  $P < 0.05$ ; Fig. 3b).

Life history trait classifications for 42 native fishes in the lower Sabine River included a continuum of soft classifications in which most species were nearest to the opportunistic strategist end point. Hard classifications included 21 opportunistic, 3 periodic, 1 equilibrium, and 17 intermediate strategists (Table 2). Occurrences of these species shifted between Periods 1 and 2, and assemblage composition significantly differed between periods (ANOSIM  $R = 0.52$ ,  $P < 0.01$ ). Two-dimensional NMDS plots illustrated separation of collections by period along NMDS 1 (Fig. 4a), including separation of species scores within NMDS space (Fig. 4b). Regression GAMs fit to the relationship between NMDS 1 and strategy end-point weights differed among end-point strategies. There was a significant relationship between NMDS 1 and strategist weights for the opportunistic end point (estimated  $df = 9$ , reference  $df = 9$ ,  $\chi^2 = 24.09$ ,  $P < 0.01$ , deviance explained = 47.5%) characterized by a general reduction in strategist weight among fishes with higher NMDS 1 scores (Fig. 5a). There was no relationship between NMDS 1 and strategy weights for the periodic end point (estimated  $df = 9$ , reference  $df = 9$ ,  $\chi^2 = 4.10$ ,  $P = 0.905$ , deviance explained = 12.5%; Fig. 5b). There was a significant relationship between NMDS 1 and strategist weights toward the equilibrium end point (estimated  $df = 9$ , reference  $df = 9$ ,  $\chi^2 = 17.34$ ,  $P < 0.05$ , deviance explained = 38.0%) characterized by general increase in strategist weight among fishes with higher NMDS 1 scores (Fig. 5c).

Change in fish assemblage composition and life history strategist occurrences based on hard classifications revealed a reduction in opportunistic strategists but little change in intermediate strategists through space and time. The first level of hierarchically fitted GAMMs included the relationship between time and distance downstream of the dam. There was a significant effect of period for opportunistic strategists ( $t = 6.15$ ,  $P < 0.01$ ) but not for intermediate strategists ( $t = 0.24$ ,  $P = 0.812$ ). The second level in our hierarchy included fitting a GAMM to the relationship between opportunistic strategist richness and distance downstream of the dam for each period independently because of the significant effect of period in the first-level model. The smoothing term for distance downstream of the dam was significant for Period 1 (es-



**Fig. 3.** Principal component (PC) biplots illustrating indicators of hydrologic alteration flow regime attributes measured annually for the period 1927–2007 at USGS gages near (a) Bon Weir, Texas, and (b) Ruliff, Texas. Variation explained by each PC axis is given as a percentage. Temporal panels on the right illustrate changes in annual scores along PC 1 (upper) and PC 2 (lower). Construction of Toledo Bend Reservoir was completed in 1967 (gray bar), after which PC 2 scores declined significantly until 1982 when fish assemblage census data ceased (solid line = linear fit; dashed lines = 95% confidence interval; see text). Highly correlated flow attribute names are jittered for clarity.

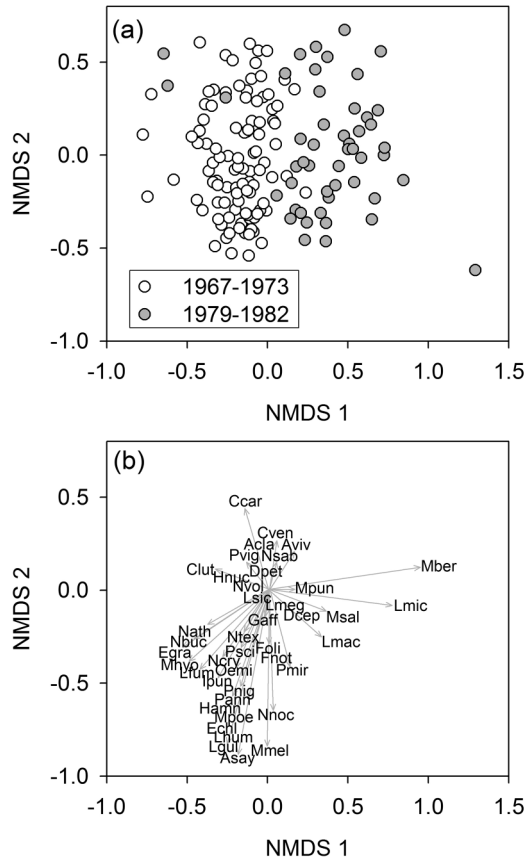


timated  $df = 3.21$ , reference  $df = 3.21$ ,  $F = 4.71$ ,  $P < 0.01$ , adjusted  $R^2 = 0.19$ ) but not for Period 2 (estimated  $df = 1.00$ , reference  $df = 1.00$ ,  $F = 2.53$ ,  $P = 0.118$ , adjusted  $R^2 = 0.03$ ). Differences between smoothing function shapes indicated 8–17 opportunistic strategists were predicted throughout the 250 km segment of river during Period 1, but predicted richness was reduced to 3–6 during Period 2 (Fig. 6a). Because the first-level model indicated no effect of period for intermediate strategists, we retained the combined periods for intermediate strategists to illustrate longitudinal variation. The smoothing term for distance was not significant (estimated  $df = 5.25$ , reference  $df = 5.25$ ,  $F = 1.86$ ,  $P = 0.061$ , adjusted  $R^2 = 0.05$ ), and the predicted number of intermediate strategists ranged 3–6 throughout the 250 km segment of river (Fig. 6b).

Strategist richness was related to the PC 2 flow function for opportunistic but not intermediate strategists. The GAMM fit to

opportunistic strategist richness included a significant smoothing term for PC 2 (estimated  $df = 1.00$ , reference  $df = 1.00$ ,  $F = 70.89$ ,  $P < 0.01$ , adjusted  $R^2 = 0.32$ ), but the PC 2 smoothing term was not significant for intermediate strategists (estimated  $df = 1.00$ , reference  $df = 1.00$ ,  $F = 1.35$ ,  $P = 0.248$ , adjusted  $R^2 = 0.01$ ). Differences between GAMM fits and smoothing functions illustrated an increase in opportunistic richness from on average four strategists for negative PC 2 flow function scores (i.e., least variable flows) to on average 11 strategists for positive PC 2 flow function scores (i.e., most variable flows). Predicted intermediate strategist richness values ranged 2–4 across the gradients of PC 2 flow function scores (Fig. 7a). We illustrated the temporal sequence of change in strategist richness and PC 2 flow function scores by plotting fitted values in the order in which they occurred between 1967 and 1982. Through time, opportunistic strategist richness was three times

**Fig. 4.** Two-dimensional nonmetric multidimensional scaling (NMDS) biplots illustrating (a) ordinated distances for fish assemblage samples collecting during 1967–1973 (open circles) and 1979–1982 (gray circles) and (b) species scores (see Table 1 for species codes; some vectors are not shown for clarity).

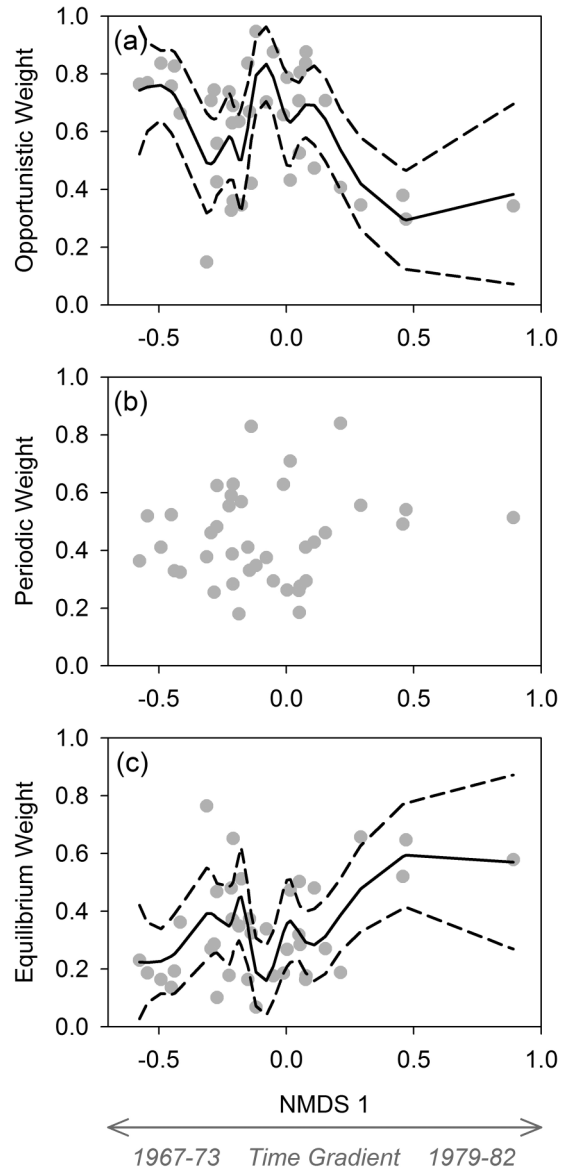


greater than intermediate strategist richness during 1967 but declined until 1982 when, on average, the same number of opportunistic and intermediate strategists were present (Fig. 7b).

**Discussion**

Our study provides empirical evidence for the spatiotemporal scaling of ecological consequences associated with impoundment construction and flow regime alteration. Following completion of TBR, stream flow magnitudes were relatively unchanged during the next decade, despite significant reduction in flow variability. PCA results illustrated conversion from flows characterized by “higher highs”, “lower lows”, minimal base flow, and high annual CV prior to impoundment, to flows characterized by “lower highs”, “higher lows”, augmented base flows, and reduced annual CV following impoundment. This form of flow homogenization is characteristic of dam operations that optimize hydropower production (Poff et al. 1997; Gido et al. 2013) and is widely reported as an agent of fish assemblage change in regulated rivers (Poff and Zimmerman 2010; Poff et al. 2010; Liermann et al. 2012). In the lower Sabine River, NMDS and ANOSIM results illustrated significant change in assemblage composition coincidental with completion and operation of TBR. Based on reduced flow variability, life history theory predicts that opportunistic strategists should be negatively affected while equilibrium strategists should be positively affected (Winemiller and Rose 1992; Olden and Kennard 2010; Mims and Olden 2012). We found that strategy weights for the opportunistic end point were relatively large during Period 1 and declined across the NMDS 1 time gradient, whereas strategist weights for the equilibrium end point were relatively small dur-

**Fig. 5.** Relationship between NMDS axis 1 scores and the probability of species being classified as (a) opportunistic, (b) periodic, and (c) equilibrium life history strategists. Fitted values (solid lines) and 95% confidence intervals (dashed lines) for generalized additive models are illustrated. Strategy weights are from Mims et al. (2010; see Table 2).

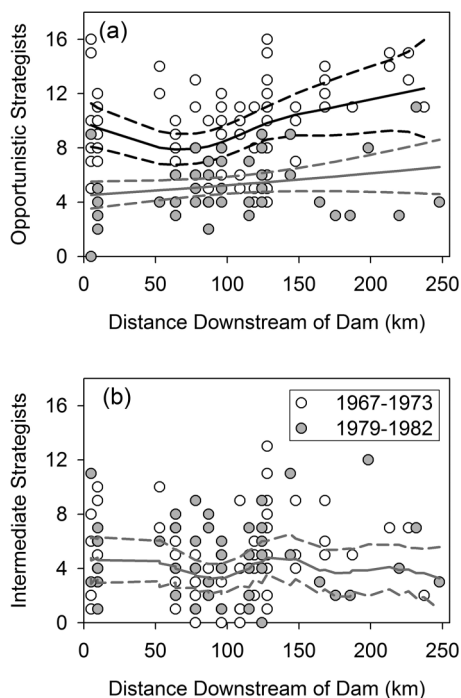


ing Period 1 and increased across the NMDS 1 time gradient. These results based on soft classifications support life history theory expectations, but do not directly relate the spatiotemporal extent of fish assemblage change to TBR. When we used hard classifications to consider the effect of time period combined with the effect of longitudinal distance downstream of TBR, we found that opportunistic strategist richness underwent a nearly uniform reduction along 250 km of river between periods, while intermediate strategist richness remained constant through space and time. The opposing responses by opportunistic and intermediate strategists was echoed with regard to change in flow variability, in that opportunistic strategist richness declined following impoundment construction and flow homogenization while intermediate strategist richness remained constant. Collectively, our findings provide empirical support for the link between flow regime alteration and directional change in stream fish assemblage composi-

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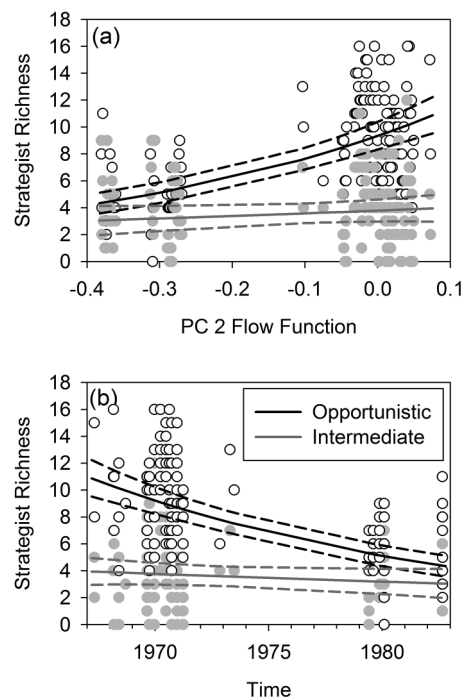
**Fig. 6.** Relationship between downstream distance from Toledo Bend Dam and richness of (a) opportunistic strategists and (b) intermediate life history strategists for collections made during 1967–1973 (open circles) and 1979–1982 (gray circles). Regression lines illustrate fitted values (solid lines) and 95% confidence intervals (dashed lines) for generalized additive models applied to opportunistic species richness during 1967–1982 (black lines) and 1979–1982 (gray lines).



tion as mediated by life history strategies and highlight the broad spatial but fine temporal extent over which alteration to natural environmental filtering can manifest.

Multiple mechanisms likely contributed to the observed pattern of fish assemblage change in the lower Sabine River. Suttkus and Mettee (2009) documented the decline and extirpation of fishes in the family Cyprinidae in the lower Sabine River and suggested altered thermal regime downstream of TBR was at least partially responsible. Degraded thermal regimes are inseparably connected to impoundments with hypolimnetic releases (Olden and Naiman 2010), and this mechanism cannot be excluded as a driver of change in the lower Sabine River. However, our findings suggest opportunistic strategist richness declined over a 250 km segment of river downstream of TBR, potentially extending the effect of altered flows beyond the footprint of dam alteration to thermal regimes and geomorphology (Phillips 2008; Fencl et al. 2015). Another factor potentially related to assemblage change included the stocking of >2.5 million equilibrium strategists (i.e., *Ictalurus punctatus* and *Micropterus salmoides*) into TBR in 1967 (TPWD 2016). A portion of these fishes might have made their way into the lower Sabine River given the known association between stocked fish dispersal and reservoirs (Johnson et al. 2008). In fact, *I. punctatus* had the highest strategist weight for the equilibrium end point (and lowest weight for the opportunistic end point) but a greater occurrence during Period 1 when stocking occurred, and this is consistent with the point with the largest residual value in Figs. 5a and 5c being related to human stocking rather than pure environmental (i.e., flow) effects. Readers should also be mindful of three limitations to our database, including the uncertainty surrounding the equality of effort allocated across space and time, the fact that seines have bias toward collection of small-bodied fishes that tend to fit the opportunistic (but not periodic or equi-

**Fig. 7.** (a) Relationship between richness of opportunistic (open circles) and intermediate (gray circles) life history strategists and the flow function fitted to PC 2 (see Fig. 3). Regression lines (solid lines) and 95% confidence intervals (dashed lines) for generalized additive mixed models (GAMMs) are fitted to opportunistic (black lines) and intermediate (gray lines) strategists. (b) Raw data and fitted GAMM relationships show in sequential order through 1967–1982. Identical points are jittered for illustration in both panels.



librium) life history strategy, and lacking pre-impoundment data. Although there is precedence for the application of data collected by Royal Suttkus to measure assemblage change because of the known rigor of the collector (e.g., Onorato et al. 2000; Suttkus and Mettee 2009; Geheber and Piller 2012), an additional point we make here is the consistency in the number of intermediate strategists collected through space and time. Intermediate strategists are not expected to respond to flow change in the same manner as opportunistic strategists under current life history theory (Mims and Olden 2013), and therefore such strategists offer a natural control for assessing changes in strategist richness across gradients of altered flow variability. In our study, the number of small-bodied intermediate strategists remained constant during a period of reduction in the more sensitive (with respect to flow variability) opportunistic strategy. With respect to the bias of seines toward small-bodied fishes, we believe this bias to be acceptable within the context of our study given our focus on opportunistic strategists, which (i) are sensitive to the dominant form of flow change in the lower Sabine River and (ii) represent the dominant life history strategy in the region (Mims et al. 2010). Finally, limited pre-impoundment fish collections did not allow for a before–after analysis in which the unaltered, historical assemblage was used as a benchmark to measure change following impoundment. Although our analyses detected considerable change in assemblage composition in the years immediately following impoundment, this change might be conservative with respect to total magnitude of change in opportunistic fish abundances. However, based on long-term hydrographs and annual PCA scores for flow gradients, the beginning of our study period captured the transition of flows from unregulated to impoundment-regulated, and our temporal extent is therefore appropriate for testing ecological responses to altered hydrology.

Existing empirical evidence for theoretical relationships between stream flows and life history traits was largely derived from comparative, among-basin or among-site studies. Multiple comparative works report positive relationships between flow variability and opportunistic strategists, seasonal flow regimes and periodic strategists, and stable flow regimes and equilibrium strategists (Tedesco et al. 2008; Olden and Kennard 2010; Mims and Olden 2012). The mechanistic underpinning for the association between flow variability and opportunistic strategists is related, at least in part, to the capacity of short-lived and early-maturing species to exhibit rapid population growth and recolonization following disturbances (Schlosser 1990; Winemiller and Rose 1992). Periodic strategists benefit from seasonal access to floodplain spawning habitats that strongly regulate recruitment (Winemiller 2005; Stoffels et al. 2016), while equilibrium strategists benefit from low fecundity and high parental investment necessary for strong recruitment in stable environments where biotic interactions outweigh abiotic processes (Townsend 1989; Jackson et al. 2001). Based on these patterns, we predicted that reduced flow variability following TBR would result in reduced occurrence of opportunistic strategists and increased occurrence of equilibrium strategists. Although our predictions are not novel, our approach and scale of observations used to test predictions are innovative. Previous applications of time series data to test life history theory were confounded by interactions among hydrology, non-native species invasions, or changes in collector identities and methods through time (Olden et al. 2006; Gido et al. 2013). Our study used rarely available time series data collected by the same individual, using the same methodologies, and targeting the same sites during a period of environmental change that preceded biological invasions. Despite the previously described limitations in the data set, our approach allowed for testing life history theory predictions at an unprecedented, intermediate spatial scale (sensu Fausch et al. 2002) while avoiding the issue of identifying dam-influenced and non-dam-influenced sites (Mims and Olden 2013). Our results suggest the influence of impoundment construction on trait filtering can extend hundreds of kilometres downstream and affect entire river segments (Fausch et al. 2002). This finding fills a void in spatial scaling not captured by broader, continental-scale approaches that emphasize measuring the spatial replication rather than the spatial extent of filtering (Mims and Olden 2012; McManamay and Frimprong 2015). This finding represents a critical step forward in the management of river-scapes by highlighting the potential for limited recovery along a longitudinal gradient >250 km in length downstream of an impoundment (Kinsolving and Bain 1993; Pyron and Lauer 2004). Because the lower Sabine River is isolated, there is little opportunity for fish colonization from other adjacent large rivers. This means that our study area was simultaneously afflicted by fragmentation and flow alteration, and a growing body of literature suggests the effects of flow alteration are amplified in the presence of isolating fragmentation and can result in irreversible assemblage change (Perkin et al. 2015a, 2015b). Finally, our study highlights the fine temporal extent over which environmental filtering can manifest. Existing broadscale tests of life history theory assess “contemporary” fish–flow relationships using hydrologic metrics calculated with at least 15 years of data (Mims and Olden 2012; McManamay and Frimprong 2015). Our findings suggest transformation of fish assemblages can occur within this window of time, especially if assemblages are dominated by opportunistic strategists. This raises new research questions regarding the temporal extent over which life history strategists respond to environmental filtering, though it is evident from our results that change caused by strategist loss can manifest over ecological (as opposed to evolutionary) time scales. Our findings suggest management of flows to benefit conservation or management of native fish assemblages should, at a minimum, incorporate consideration of flow variability.

Development of flow standards for regulated rivers requires linkages between ecological traits of organisms and stream flow gradients. A core concept in the science of “environmental flows” is the ecological limits of hydrologic alteration (ELOHA), a framework that guides development of ecologically sustainable flow management (Poff et al. 2010). The central tenant of ELOHA is that relationships between hydrologic alteration and ecological responses should guide flow management decisions, and life-history-trait-based ecological responses are a promising avenue for establishing the necessary flow–ecology relationships. One limitation to the ELOHA framework involves flow-degraded ecosystems with limited opportunities for recolonization by extirpated species following restoration of appropriate flows (McManamay et al. 2013). Given the apparent extirpation of many fishes from the lower Sabine River and subsequent reduction of opportunistic strategists (Suttkus and Mettee 2009; this study), restoration of the natural fish assemblage in the lower Sabine River might require reintroduction of missing species from genetically appropriate sources (e.g., Osborne et al. 2014). For the remaining opportunistic strategists, large-scale flow experiments targeting return of natural flow variation would allow for application of the ELOHA framework (Poff et al. 2010). Flow experiments timed with natural environmental variation (e.g., deluge events) are a recently proposed approach for quantitatively testing the ecological benefits associated with natural flow regime mimicry in regulated rivers (Konrad et al. 2011; Olden et al. 2014). Our study provides direction for the flow regime attributes, ecological responses, and spatiotemporal scales of investigation that might be included in flow experiments targeting solutions to ecological consequences associated with anthropogenic flow modifications (Richter et al. 2003; Poff et al. 2010). Although our study focused only on one regulated river, the global distribution of dams and opportunistic life history strategists suggest the empirical support we documented for life history theory is likely to be applicable to other regions where impoundment construction has already occurred or is expected to occur in the future (Olden and Kennard 2010; Lehner et al. 2011).

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