Hydrobiologia
https://doi.org/10.1007/s10750-021-04514-z

PRIMARY RESEARCH PAPER

Spatial and temporal dynamics of fish assemblages in a desert reservoir over 38 years

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Received: 20 October 2020 / Revised: 18 December 2020 / Accepted: 6 January 2021

Abstract Processes associated with reservoir aging threaten the capacity of systems to continue providing productive fisheries, and declining productivity might be exacerbated by decreasing water level associated with climate change and water abstraction. Despite their prevalence in riverscapes, we know little about long-term fish dynamics in reservoirs. Using a 38-year dataset from Lake Powell, USA, we tested for changes in assemblage structure and changes in fish condition for the most abundant species. The assemblage has undergone re-ordering of species relative abundance, but the same core species captured in 1981 were still present in 2018. Five species increased in relative abundance, while two declined, and seven remained unchanged. Walleye *Sander vitreus* and Smallmouth Bass *Micropterus dolomieu* were among those increasing over time, while Channel Catfish *Ictalurus punctatus* and Common Carp *Cyprinus carpio* declined. We were not able to attribute changes in fish assemblages with a suite of abiotic and biotic variables. Condition was low and declined over time for four of the six species. Although water level declined over time, we did not observe obvious declines in basal food resources. Declining water level has reduced availability of littoral habitat and likely contributed to declines in some species associated with this zone.

Keywords Community · Stability · Non-native species · Colorado river · Long-term data

Handling editor: Andrew Dzialowski

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-021-04514-z.

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Introduction

Reservoirs are human-engineered habitats in riverscapes across the globe and provide important societal benefits, such as water storage, hydroelectric power, and economically important recreational and commercial fisheries. These novel habitats have been constructed in nearly every major river basin, and many are still being constructed in countries or areas that were previously un-impounded (Grill et al., 2019). Many were built recently (< 80 years), but it is not clear how biological communities in these systems will respond over time. For instance, reservoir construction began in North America in the early

Published online: 13 February 2021

nineteenth century and reached a peak in the 1970s-80 s (Rosenberg et al., 2000). Many reservoirs are reaching critical limits of sedimentation, resulting in declines in reservoir volume and changes in habitat (Juracek, 2015; George et al., 2017). In the western United States, declining reservoir water levels are the result of increased water use and persistent regional drought that have been exacerbated by climate change (Milly & Dunne, 2020; Williams et al., 2020). Despite the commonness of reservoirs, we know relatively little about long-term assemblage dynamics in these novel, highly variable ecosystems (Hrbáček et al., 2003; Irz et al., 2006; Gao et al., 2019).

Reservoirs exhibit high intra- and interannual variability in habitat conditions, such as water levels (e.g., Murphy et al., 2019) that are driven by both river basin hydrology and water management (Christensen et al., 2004; Dawadi & Ahmad, 2012; Eloranta et al., 2018). Reservoir aging is also thought to result in predictable changes in productivity, which are linked to changes in fish production (Trophic Surge Hypothesis; Turgeon et al. 2016; Monaghan et al. 2020). After dams close and reservoirs fill, these systems experience a period of increasing productivity as terrestrial habitat is initially inundated (the "surge" phase; Jenkins, 1967; Kimmel & Groeger, 1986; Turgeon et al. 2016). For example, fisheries are highly productive during the initial years of reservoir filling when trophic resources and habitat availability (e.g., inundated terrestrial land; trees) are highest (Shelton et al., 1979; O'Brien, 1990; Miranda & Bettoli, 2010). Productivity generally peaks after reservoirs fill to capacity and then falls (i.e., trophic "depression" phase; Turgeon et al. 2016) as systems switch to being dominated by internal nutrient cycling (Jenkins, 1967; Ploskey, 1981; Kimmel & Groeger, 1986). Spatial variation in depth and terrestrial inputs from inflowing rivers can lead to gradients in nutrient availability and primary production causing a trophic depression, or decreased ecosystem productivity, particularly in lacustrine habitats nearer the dam over time (Thornton et al., 1990). Although inflowing rivers continue to provide external nutrient loading, these resources are used rapidly by primary producers in transitional zones at the upstream end of reservoirs (Thornton et al., 1990). Consequently, transitional habitats have relatively higher primary and secondary productivity, and fish densities are highest near river inflows (Mueller & Horn, 2004; Vašek et al., 2004; Lin et al., 2019).

Conversion of lotic to lentic habitats as a result of dam construction causes an initial loss or displacement of native species as obligate lotic species are filtered out (Agostinho et al., 2008, 2016; Loures & Pompeu, 2019). Collectively, less is known about long-term assemblage dynamics as reservoirs continue into periods of trophic depression (Gido et al., 2000; Gao et al., 2019; Baumgartner et al., 2020). Prior research on temporal change in reservoir fish assemblages is equivocal. Despite being unstable environments, some reservoir fish assemblages can be quite stable over long time periods (i.e., > 20 years; Dolman, 1990; Gido et al., 2000; Matthews et al., 2004), while assemblages in other reservoir systems have changed substantially through species losses (e.g., Orsi & Britton, 2014) or re-ordering of species' relative abundances (e.g., Říha et al., 2009). Reservoirs often consist of a suite of species native to the region, as well as introduced non-native species (Havel et al., 2005; Johnson et al., 2008a, b). In North America, populations of introduced sport fishes, mostly predatory species, tend to decline as reservoirs age (Kimmel & Groeger, 1986; Miranda & Durocher, 1986; Ploskey, 1986). Many native and introduced fish species that remain past the initial formation and filling of the reservoir are omnivorous and habitat generalists, and so might be better adept to deal with highly dynamic habitat conditions in reservoirs (Matthews et al., 2004; Buckmeier et al., 2014; Vašek et al., 2016).

Long-term datasets are difficult and costly to build, but are essential for assessing community dynamics; providing a means of establishing baseline conditions to which future changes can be compared (Gido et al., 2000; Matthews & Marsh-Matthews, 2016; Lamothe et al., 2018). Our objective was to test for long-term (38 years) changes in the Lake Powell fish assemblage using data collected at four sites across the reservoir. Specifically, we were interested in testing for directional changes in fish assemblage composition and relative abundance, and changes in fish condition over time. We assessed fish assemblages of the fish assemblage starting two years after the reservoir first filled; thus, when the reservoir was potentially first entering a trophic depression phase (e.g., Turgeon et al., 2016). We expected reservoir aging would lead to declines in catch rates, total fishes captured, fish condition, and declines in relative abundance of

predatory sport fishes as seen in other systems (Kimmel & Groeger, 1986; Miranda & Durocher, 1986; Ploskey, 1986). We also predicted assemblages to vary spatially among sampling sites based on habitat and productivity gradients in reservoirs (e.g., Okada et al., 2005; Ferrareze et al., 2014; Baumgartner et al., 2018). Finally, we predicted that declines in water level would have a relatively larger impact on littoral-associated species than pelagic-associated species as the amount of littoral habitat declines. Although inconsistent collection of other abiotic and biotic variables potentially contributing to changes in the fish assemble precluded us from assessing mechanistic drivers over the whole time series, we were able to assess long-term trends in these variables for a portion of the time series (22 years) at one site, and we discuss these patterns in relation to observed changes in the fish assemblage.

Materials and methods

Study area

Lake Powell is a large reservoir (volume: over 33 billion m^3; surface area: over 65,300 ha; https://www.usbr.gov/projects/index.php?id=144) formed by Glen Canyon Dam on the Colorado River near Page, Arizona. The reservoir inundates ~ 300 km of the Colorado River upstream into southern Utah. Glen Canyon Dam closed in 1963, and the reservoir first reached full pool on June 22, 1980. Being a canyon-bound reservoir, 53% of the shoreline of Lake Powell consists of vertical cliffs and the rest consists of talus slopes (Potter & Pattison, 1976). Thus, shoreline erosion is minimal relative to many other reservoirs that inundate more erodible soils, such as in the central USA (e.g., Severson et al., 2009). Gradients of depth, turbidity, nutrients, primary productivity, and zooplankton exist from river inflows to the dam (Paulson & Baker, 1983; Potter & Drake, 1989; Stanford & Ward, 1991; Deemer et al., 2020). The reservoir is considered oligotrophic with relatively low nutrient levels and chlorophyll *a* typically less than 2 μg L^{-1} with slightly higher concentrations near river inflows and in side canyons (Sollberger et al., 1989; Wurtsbaugh & Gallo, 1997). Water levels vary within and among years (max depth = 170 m), and over the past several decades have generally declined as demands for water have increased and drought and climate change have reduced flows in rivers across the Colorado River Basin (Fig. 1; Milly & Dunne, 2020). Water level in 2018 was approximately 20 m lower than after initial filling, which equates to a reduction in volume of approximately 12 km^3.

Intentional and unintentional species introductions have taken place since Lake Powell was formed. For instance, intentional stocking of seven fish species took place from 1963 to 1993 (Supplemental Table 1). Two species have been unintentionally introduced to Lake Powell since data collection began. Gizzard Shad *Dorosoma cepedianum* (Lesueur, 1818) colonized the San Juan River after escaping from an impoundment near the San Juan River (Mueller & Brooks 2004; Finney & Fuller 2008), and eventually were detected in the San Juan arm of Lake Powell in 2000 (Vatland & Budy, 2007). Additionally, Quagga mussels *Dreissena bugensis* (Andrusov, 1897) were first detected in Lake Powell in 2012 near the Wahweap Marina (G. Blommer, Utah Division of Wildlife Resources, personal communication).

Fish sampling

Four sampling sites were spread across the reservoir. Two sites were located near inflows of the two main rivers forming Lake Powell, the Good Hope Bay (GHB) site near the Colorado River inflow and the San Juan (SJ) site near the San Juan River inflow (Fig. 1). One site was centrally located along the longitudinal axis of the Colorado River arm, the Rincon (RN) site, and the last site was located close to the dam, Wahweap (WW). We analyzed data from when sampling began in 1981, nearly two years after the reservoir first filled to capacity, to 2018. Data were collected annually in the fall (late October through early November) using standardized gill net surveys. Nets were deployed at each site for one or two consecutive nights. Generally, 10 monofilament experimental, sinking gill nets were deployed each afternoon and retrieved the following morning. Each 30.5 m net consisted of four panels (7.6 m long × 1.8 m tall) with progressively increasing bar mesh sizes of 19, 25, 38, and 51 mm. Nets were attached to the shore, alternating large and small mesh panels towards the inshore side. Captured individuals were counted, and a subset measured for total length (TL, mm) and weight (g).

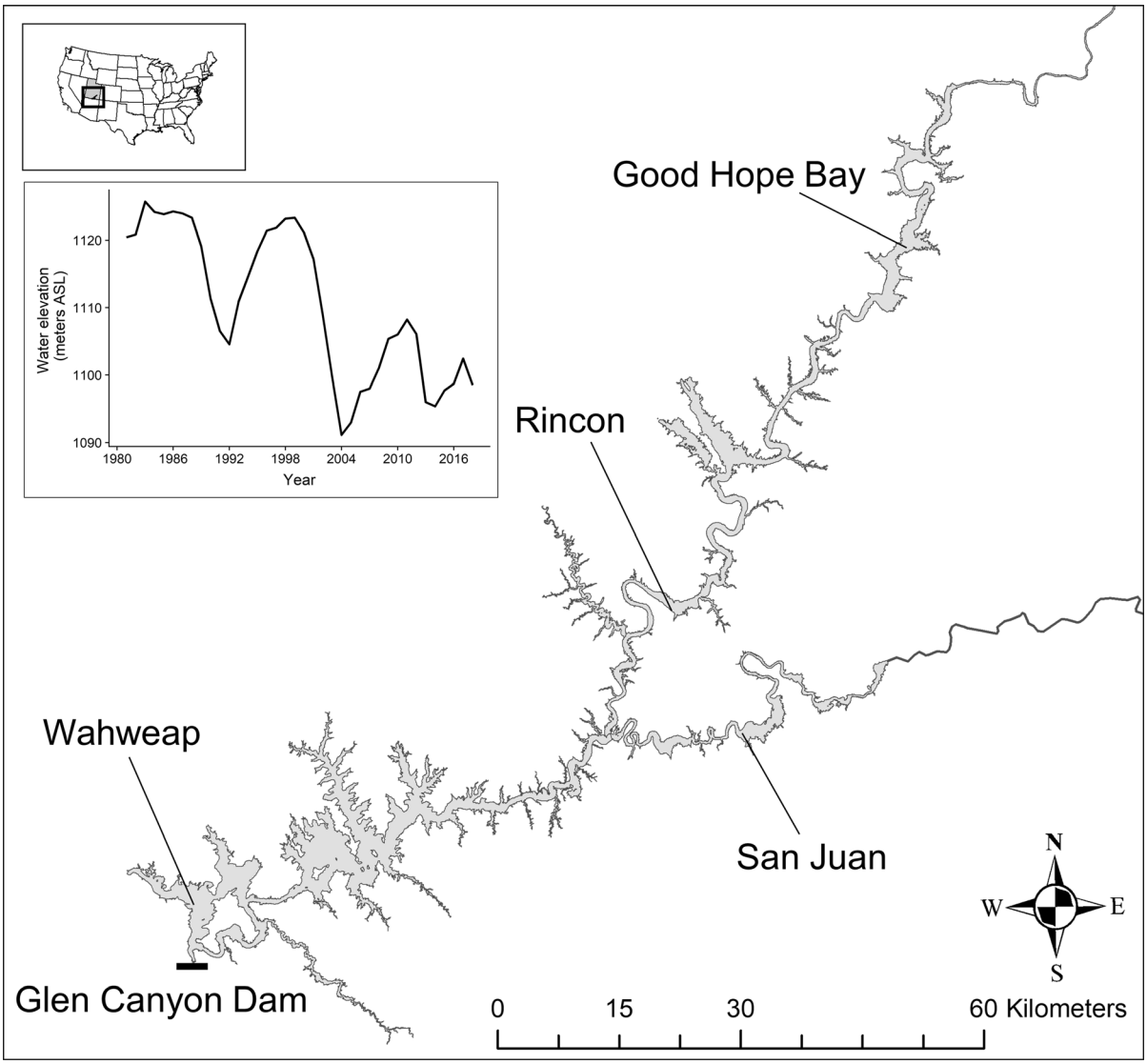

Fig. 1 Study area map of Lake Powell, Utah and Arizona. Four sites were sampled across the reservoir including one in each tributary arm (Good Hope Bay; GHB and San Juan; SJ), one mid-reservoir (Rincon; RN), and one near the dam (Wahweap; WW). Inset shows reservoir water elevation over the course of the study

Abiotic and biotic variables

We lacked consistent abiotic and biotic data over the time series that might contribute to fish assemblage change. However, we were able to obtain data on water temperature (within 1.5 m depth), phytoplankton biovolume (within 1 m depth), zooplankton biomass (30 m tow), and nitrite + nitrate (NO_{2-} + NO_3-N; averaged across samples from major strata) collected at the site nearest the dam (WW) from 1993 to 2014 (Vernieu, 2015a, b). Data on soluble reactive phosphorus were also collected, but the detection limit changed over the time series (C. Yackulic, U.S. Geological Survey, personal communication). For this reason, and because soluble reactive phosphorus was correlated with nitrite + nitrate (r = -0.57, P = 0.006), we excluded phosphorus from further analyses. These data were part of water quality monitoring efforts conducted by the U.S. Bureau of Reclamation, Glen Canyon Environmental Studies program, and U.S. Geological Survey (*see* Vernieu, 2015a, b for specific methodology). We averaged data

across samples for each year except for water temperature, which we used average summer temperature (July–September). We also compiled average annual water elevation (m) for these same years.

Statistical analyses

All analyses were performed in program R, version 3.5.3 (R Core Team, 2019). Fish captures in gill nets were summed across individual nets at a site in each year, which we considered to be a sample. Although there was some variation in the number of nets set per site per year (range: 8–20 nets), 85% of samples consisted of 20 nets. We used generalized linear models (GLM) to test for changes over time in total catch per unit effort (CPUE), number of species captured per unit effort (species CPUE), and evenness (Pielou, 1966). We assumed a Gamma distribution (link = inverse) because values were positive-only and continuous. Because Gizzard Shad did not occur until 2000, and then became highly abundant and ubiquitous in the reservoir (Vatland & Budy, 2007), we ran models with and without Gizzard Shad. For univariate responses, we made pairwise comparisons among sites using Tukey's HSD if the interaction term was not significant ($\alpha = 0.05$). For analysis of long-term change in community structure, we removed Gizzard Shad and rare species that were present in < 3% of samples. Removing Gizzard Shad from the analyses allowed us to test for changes in the community that might have resulted from their introduction. We retained 13 species for the assessment of long-term change in fish assemblages.

A multivariate generalized linear model (manyGLM; Wang et al., 2012, 2019) was used to test for spatial and temporal variation in fish assemblage structure. This approach is a model-based equivalent to distance-based multivariate methods such as PERMANOVA (Anderson, 2001; Wang et al., 2012), which allows the original structure of the data (e.g., counts, presence–absence) to be maintained rather than transforming data into a distance matrix. We modeled species counts per site per year assuming a negative binomial distribution (link = log) and accounted for variable effort within the model by including the number of net nights as a covariate. This allowed for correction for variable effort within the model rather than prior to by transforming data to catch per unit effort, but still resulted in a measure of species abundance corrected for effort (i.e., relative abundance). Time, site, and their interaction were included as effects of interest in the model. Effects of site were included because previous research in reservoirs has found longitudinal differences in fish catch rates (Matthews et al., 2004; Vašek et al., 2004; Okada et al., 2005), and the four sites assessed in this study were spread across the reservoir. The manyGLM model routine fits a GLM for each species using the same set of predictor variables (Wang et al., 2019). The likelihood ratios (*LR*) from species-specific GLMs are summed together (i.e., *Sum-of*-LR), and these are used to test for assemblage-level effects with *P* values estimated via resampling ($n = 9999$ iterations; Wang et al., 2012). Significance of species-specific GLMs are then determined by permutation-based ANOVA, and *P* values are corrected for multiple testing. Contributions of each species to assemblage-level effects can be calculated by dividing the *LR* of species-specific models by the *Sum-of-LR*, similar to a SIMPER analysis (Clarke, 1993). Although fish populations can exhibit non-linear patterns (e.g., predator–prey cycles; Vatland & Budy, 2007), GLMs should be able to identify strong linear trends (increases or decreases) over time. Statistical significance was assessed at an $\alpha = 0.05$.

To test for effects of abiotic and biotic variables on fish assemblage structure for a subset of the time series that data were available, we again used a multivariate GLM. We used principal component analysis (PCA) to summarize biotic and abiotic variables at the WW site. Axes from PCA indexed interannual variation in biotic and abiotic variables in the proceeding analysis. Our biotic and abiotic variables were the first three axes derived from PCA, which described 84% of the interannual variance in these variables at the WW site (Supplemental Fig. 1). We modeled species counts at the WW site from 1993 to 2014 assuming a negative binomial distribution as described above. We included the three PCA axes as predictor variables in the model, and included the effect of year to account for changes over time. Effort (net nights) was equal across years for this subset of data so, we did not include the effect of effort in the model. We tested for assemblage-level effects using resampling as described above. Finally, we quantified trends in these variables over time using generalized additive models (GAM; Wood, 2011). To test for trends over time, we fit models including a smoothing term of year using the "gam" function in

the mgcv package (Wood, 2017), and assumed a Gamma distribution (link = log).

To assess changes in fish condition over time, we calculated relative weights (*Wr*) for six species that had consistent length and weight data over the majority of the time series. *Wr* is a commonly calculated condition index based on a standard weight equation for a species from individuals from many populations over a broad spatial and temporal extent (Neumann et al., 2012). This metric provides useful information to managers by providing an index of condition that can be compared across waterbodies. A *Wr* of 100 represents a fish in good condition (75th percentile) relative to others across the species' range. We used standard equations reported in Neumann et al. (2012) to calculate *Wr* (Supplemental Table 2). We removed any individuals smaller than the minimum reported to build standard equations. Because this dataset contains 1000 s of data points per species, the power to detect changes over time was high when using individual fish as replicates. To avoid inflating power of statistical tests, we used the average yearly *Wr* as a response variable in least squares regressions, which limited the maximum number of data points to 38 for species collected and measured in every year of the study. We tested for changes in *Wr* over time by using year as the independent variable. Assumptions of normality and heteroskedasticity were checked with residual plots, and no major violations were apparent.

Results

A total of 34,966 individuals consisting of 20 species was captured over the entire study period with gill nets set for the equivalent of 26,435 net nights (Table 1). Striped Bass *Morone saxatilis* (Walbaum, 1792) was the most abundant species, representing 35% of the total catch, and were present at every site in every year (Table 1). Walleye *Sander vitreus* (Mitchill, 1818), Largemouth Bass *Micropterus salmoides* (Lacépède, 1802), Common Carp *Cyprinus carpio* Linnaeus, 1758, and Channel Catfish *Ictalurus punctatus* (Rafinesque, 1818) occurred in > 95% of samples, while Flannelmouth Sucker *Catostomus latipinnis* Baird & Girard, 1853 and Razorback Sucker *Xyrauchen texanus* (Abbott, 1860), two native species, occurred in 21 and 13% of samples, respectively (Table 1). There was a significant interactive effect of site and year on total CPUE in models without (GLM; $F_{3,144} = 5.00$, $P = 0.003$) and with Gizzard Shad ($F_{3,144} = 5.08$, $P = 0.002$; Table 2). Total catch per unit effort increased at the GHB site over time, regardless if models included Gizzard Shad or not (Supplemental Fig. 2). Total CPUE was relatively constant at the RN and SJ sites when Gizzard Shad were excluded, but increased at the SJ site after 2000 when Gizzard Shad were included. At the WW site, total CPUE declined over time regardless of Gizzard Shad inclusion (Supplemental Fig. 2). There was no significant interactive effect of site and year on species CPUE regardless of Gizzard Shad inclusion (both $P > 0.130$; Table 2). The main effect of site was significant regardless of Gizzard Shad inclusion as well (both $P < 0.001$; Table 2), whereby the GHB site had significantly higher species CPUE (mean ± SE; 0.64 ± 0.03) than the other three sites (Tukey's HSD: all $P < 0.006$; Supplemental Fig. 2). Species CPUE at the SJ site was significantly higher (0.52 ± 0.02; $P = 0.03$) than the RN site (0.44 ± 0.02) when Gizzard Shad were excluded, but the SJ, RN, and WW sites did not differ significantly (grand mean = 0.47 ± 0.02; all $P > 0.05$) when Gizzard Shad were included. The main effect of year on species CPUE was only significant when Gizzard Shad were included in the model (Table 2). When Gizzard Shad were excluded, evenness differed among sites ($F_{3,144} = 5.08$, $P = 0.002$), was not changing appreciably over time ($F_{1,144} = 3.60$, $P = 0.060$), and there was not a significant interactive effect of site and year ($F_{3,144} = 1.24$, $P = 0.297$; Table 2). Evenness was significantly highest at the RN (0.76 ± 0.02) and SJ (0.72 ± 0.02) sites (all $P < 0.02$) compared to the GHB and WW sites (both 0.65 ± 0.02). When Gizzard Shad were included in the model, there was a significant interactive effect of site and year on evenness ($F_{3,144} = 4.27$, $P = 0.006$; Table 2), which was mainly driven by evenness at the SJ site declining after the species was detected in 2000 (Supplemental Fig. 2).

There was significant directional change in species counts (corrected for effort) over time that differed among sites (Table 3). At the assemblage level, both main effects of year ($LR = 199.5$, $P < 0.001$) and site ($LR = 400.2$, $P < 0.001$) were significant, and so was their interactive effect ($LR = 83.1$, $P = 0.001$). The significant interaction was driven by the response of

Table 1 Summary of data from gill net captures across four sites in Lake Powell from 1981 to 2018. Percent occurrence is the proportion of samples a species was collected

Species	Percent occurrence	Total captured	Mean (SD) captured per site per year
Striped Bass *Morone saxatilis* (Walbaum, 1792)	100	12,363	81.3 (65.5)
Smallmouth Bass *Micropterus dolomieu* Lacépède, 1802	88	4511	33.9 (28.2)
Walleye *Sander vitreus* (Mitchill, 1818)	99	3568	23.8 (31.6)
Common Carp *Cyprinus carpio* Linnaeus, 1758	99	2247	15.0 (14.7)
Channel Catfish *Ictalurus punctatus* (Rafinesque, 1818)	99	1547	10.3 (7.0)
Largemouth Bass *Micropterus salmoides* (Lacépède, 1802)	96	1560	10.7 (10.4)
Green Sunfish *Lepomis cyanellus* Rafinesque, 1819	73	410	3.7 (2.6)
Black Crappie *Pomoxis nigromaculatus* (Lesueur, 1829)	46	570	8.1 (13.9)
Threadfin Shad *Dorosoma petenense* (Günther, 1867)	42	466	7.3 (10.4)
Bluegill *Lepomis macrochirus* Rafinesque, 1810	66	307	3.0 (3.6)
Yellow Bullhead *Ameiurus natalis* (Lesueur, 1819)	48	190	2.6 (1.8)
Flannelmouth Sucker *Catostomus latipinnis* Baird & Girard, 1853	21	50	1.6 (1.0)
Razorback Sucker *Xyrauchen texanus* (Abbott, 1860)	13	33	1.7 (0.9)

A sample was considered to be captures from all nets deployed at a site each year

Other species captured (total) not included in multivariate analyses: Gizzard Shad *Dorosoma cepedianum* (Lesueur, 1818) (7103), Black Bullhead *Ameiurus melas* (Rafinesque, 1820) (3), Kokanee Salmon *Oncorhynchus nerka* (Walbaum, 1792) (2), Colorado Pikeminnow *Ptychocheilus lucius* (Girard, 1856) (1), Northern Pike *Esox lucius* (Linnaeus, 1758) (1), Rainbow Trout *Oncorhynchus mykiss* (Walbaum, 1792) (1)

Table 2 Generalized linear model output testing for effects of site, year, and their interactive effect on total catch per unit effort, species captured per unit effort (Richness), and evenness (n = 152)

Metric	Factor	Without Gizzard Shad			With Gizzard Shad		
		F	P	Pseudo-R^2	F	P	Pseudo-R^2
Total catch	Site	31.98	< 0.001	0.51	25.77	< 0.001	0.54
	Year	0.52	0.474		24.70	< 0.001	
	Site × year	5.00	0.003		5.08	0.002	
Richness	Site	16.67	< 0.001	0.33	15.69	< 0.001	0.35
	Year	2.95	0.088		12.31	0.001	
	Site × year	1.91	0.131		1.32	0.272	
Evenness	Site	11.07	< 0.001	0.22	4.83	0.003	0.16
	Year	3.60	0.060		1.14	0.287	
	Site × year	1.24	0.297		4.27	0.006	

Models were ran with and without Gizzard Shad, which were first detected in 2000 and then became highly abundant and ubiquitous

Walleye, which on average increased over time at the Colorado River inflow but remained relatively constant at the other three sites (interaction term: LR = 23.61, P = 0.002; Fig. 2). Counts of five species responded significantly to linear effects of time across sites, with two species decreasing (Channel Catfish and Common Carp) and three increasing (Razorback Sucker, Smallmouth Bass *Micropterus dolomieu* Lacépède, 1802, and Yellow Bullhead *Ameiurus natalis* (Lesueur, 1819); Table 3; Fig. 2). Seven

Table 3 Multivariate GLM output for the Lake Powell fish assemblage sampled at four sites from 1981–2018

Species	Likelihood ratio (*LR*) test statistics			Percent of *Sum-of-LR*		
	Year	Site	Year × site	Year	Site	Year × site
Common Carp	**54.48**	**20.86**	9.55	**27**	**5**	
Smallmouth Bass	**51.69**	6.81	7.06	**26**		
Yellow Bullhead	**34.14**	**73.81**	3.53	**17**	**18**	
Channel Catfish	**23.12**	**41.12**	6.26	**12**	**10**	
Razorback Sucker	**14.23**	**19.16**	2.18	**7**	**5**	
Walleye	5.72	**61.43**	**23.61**		**15**	**32**
Striped Bass	5.68	**73.13**	5.79		**18**	
Threadfin Shad	4.29	7.51	6.92			
Bluegill	0.65	**19.04**	5.07		**5**	
Green Sunfish	2.28	**13.18**	3.06		**3**	
Flannelmouth Sucker	2.43	**20.59**	6.63		**5**	
Black Crappie	0.73	**38.44**	2.38		**10**	
Largemouth Bass	0.03	5.09	1.10			

Models also included the effects of net nights ($P < 0.05$) as a covariate. Significant effects ($P < 0.05$), after correcting for multiple testing, are in bold. Species are ordered based on the effect size (*LR*) for the year effect. Percent of *Sum-of-LR* is displayed for species with significant relationships ($P < 0.05$)

species showed significant differences in average relative abundance among sites, mostly associated with higher abundances near river inflows (GHB and SJ sites), but with some species showing high relative abundances near the dam at the WW site as well (Fig. 3). Specifically, relative abundance of Common Carp was 32% higher and Striped Bass was 25% higher at the WW site relative to the GHB site. Black Crappie *Pomoxis nigromaculatus* (Lesueur, 1829), Flannelmouth Sucker, and Razorback Sucker were all more abundant at the SJ site, where their relative abundance was > 85% higher compared to the other three sites. Channel Catfish were nearly twice as abundant at both the GHB and SJ sites.

Despite changes over time in some biotic and abiotic variables, we did not detect a significant statistical effect (all $P > 0.430$) of any of the PCA axes representing interannual variation in biotic and abiotic variables from 1993 to 2014 on fish assemblage structure at the WW site (Table 4). Over this time period, surface water temperature and zooplankton biomass did not notably change (both $P > 0.268$; Table 5; Fig. 4). Water elevation, phytoplankton biovolume, and nitrite + nitrate all had statistically significant smoothing terms (all $P \leq 0.006$; Table 5 and Fig. 4). Water elevation was cyclical, but on average declined over time. Phytoplankton biovolume was relatively constant from 1993 to 2001 before starting to increase. Nitrite + nitrate was cyclical and higher when water elevation was lower (Fig. 4).

On average, *Wr* declined significantly over time for four of the six species for which consistent length and weight data were available (Table 6; Fig. 5). All species had *Wr* less than 100 for the majority of the time series, but Largemouth Bass had the highest *Wr*. Common Carp and Striped Bass yearly average *Wr* were always below 100 with the exception of one year (1983) for the latter (Fig. 5). These two species *Wr* remained unchanged ($P > 0.05$) over the study (Table 6).

Discussion

Our results suggest Lake Powell might still be in a trophic non-equilibrium phase (sensu Turgeon et al. 2016) 38 years after filling, and some species declines might be due to habitat changes with declining water level. Previous studies on long-term fish assemblage dynamics in reservoirs have observed both stability in the face of unstable environmental conditions (Gido et al., 2000) and significant change (Říha et al., 2009; Orsi & Britton, 2014; Loures & Pompeu, 2019). Here, upward and downward trends in species relative abundances led to a shift in community structure driven by both increases in some predatory species and decreases in some omnivorous species. These patterns are opposite of what we expected based on previous research documenting declines in predatory species as reservoirs age (Kimmel & Groeger, 1986; Miranda &

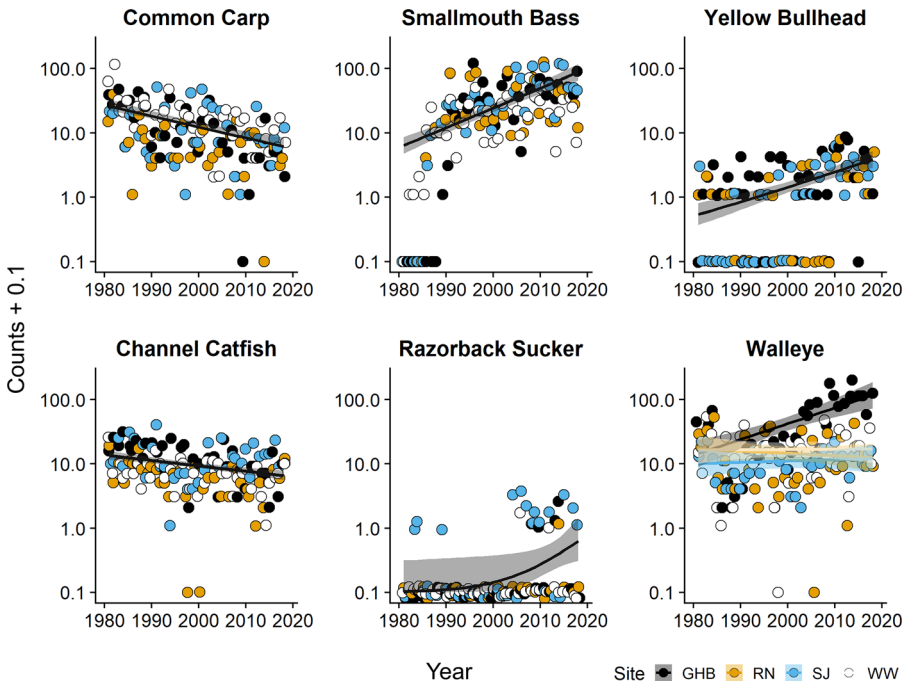

Fig. 2 Marginal means (± 95% CI) of counts for species with significant linear effects of time. Effort was corrected for within the model by including the number of nets set as a covariate, and marginal means represent counts averaged across levels of effort. Walleye had a significant site by time interaction, whereby the species increased at the Colorado River inflow (GHB) but remained generally unchanged at the other sites. Yellow Bullhead were never captured at the site nearest the dam (WW). Site abbreviations and locations are identified in Fig. 1. Panels are ordered by the effect size of year from (Table 1). *Y*-axes are on a $\log_{10}$ scale

Durocher, 1986; Ploskey, 1986), and our prediction that omnivorous species might be less affected by reservoir aging (Matthews et al., 2004; Buckmeier et al., 2014; Vašek et al., 2016). Benthic omnivores have declined in other reservoir systems; for instance, White Sucker *Catostomus commersonii* (Lacépède, 1803) declined over time in several temperate and boreal reservoirs (Turgeon et al., 2016), and benthic species are thought to be negatively impacted by habitat conditions in reservoirs in South America (Arrantes et al. 2019). The observed declines in Common Carp and Channel Catfish could be due to their association with littoral habitat, which is relatively limited in Lake Powell. Declines in water level as we observed, would serve to further reduce the amount of littoral habitat potentially leading to declines in species utilizing this zone. However, we did not find consistent responses among littoral-associated species. For example, Smallmouth Bass increased over time and Largemouth Bass displayed stable numbers. Increases or stability of some predatory fishes could have been influenced by introductions of an additional prey base (i.e., Gizzard Shad). Although the mechanisms are not immediately clear, changes in the fish assemblage coincided with long-term declines in reservoir water level. As flows in the Colorado River Basin continue to decline (e.g., Milly & Dunne, 2020), it is clear we need a more complete understanding of drivers of fish assemblage dynamics in these novel ecosystems.

Changes in native and non-native fish abundances in Lake Powell might be influenced by stocking and dispersal from upstream. For example, increasing captures of native Razorback Sucker were likely due to stocking efforts in rivers upstream of Lake Powell and subsequent movement into the reservoir (Cathcart et al., 2018; Pennock et al., 2020, 2021). Smallmouth Bass were stocked into the reservoir from 1982 to 1989 until natural recruitment was detected (Supplemental Table 1), which likely contributed to the increase in counts we observed. Conversely, intentional stocking of six other species in the reservoir did

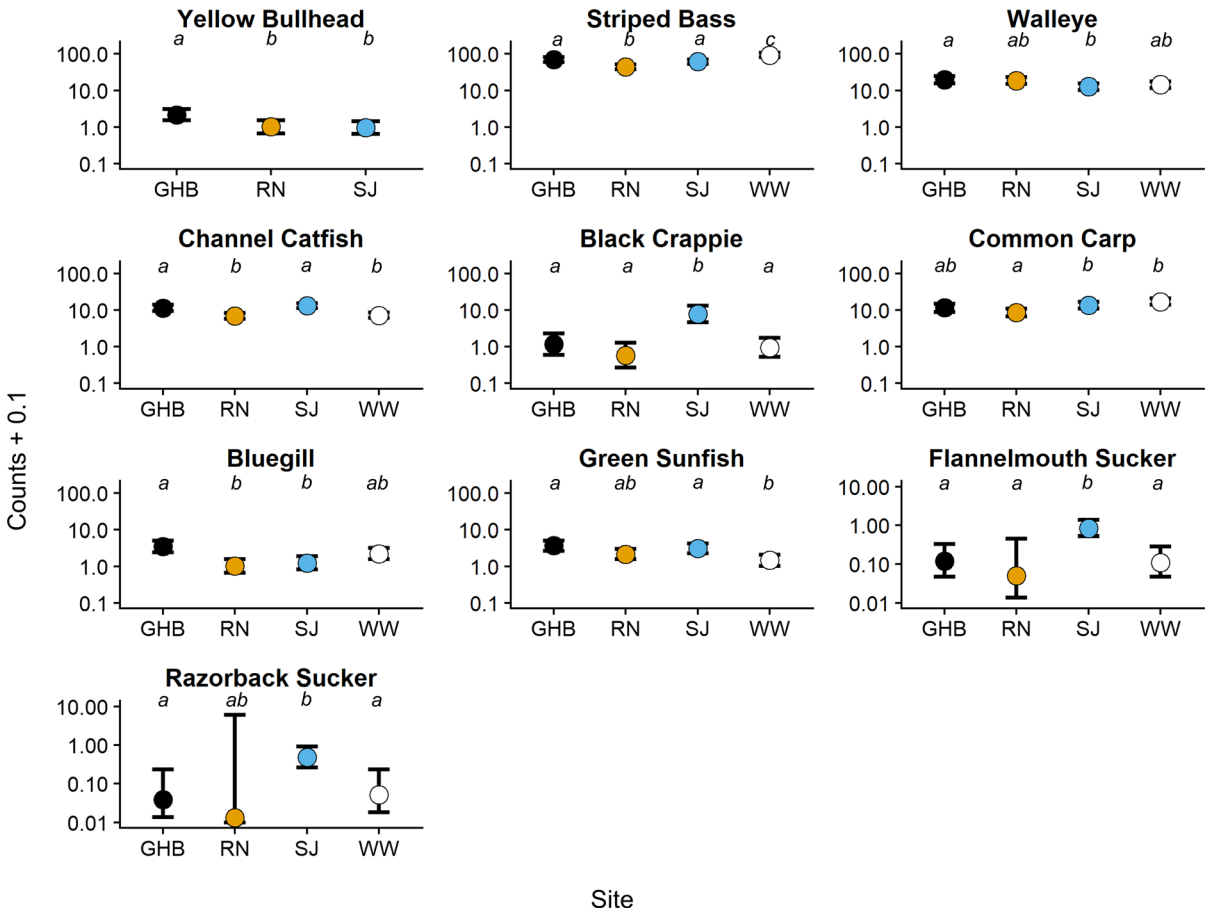

Fig. 3 Marginal means (± 95% CI) of counts (+ 0.1 or 0.01 for suckers) for species with significant effects of site. Effort was corrected for within the model by including the number of nets set as a covariate, and marginal means represent counts averaged across levels of effort and year. Walleye had a significant site by time interaction ($LR = 23.61$, $P < 0.01$), whereby the species increased at the Colorado River inflow (GHB) over time but remained generally unchanged at the other sites. Yellow Bullhead were never captured at the site nearest the dam (WW). Site abbreviations and locations are identified in Fig. 1. Panels are ordered from left-to-right by the effect size of site from Table 2. *Y*-axes are on a $\log_{10}$ scale, and are reduced for the two sucker species that were less abundant. Sites sharing the same letter did not differ significantly based on overlapping 95% CI

Table 4 Multivariate GLM output testing the effects of interannual variation in biotic and abiotic variables summarized as principle component axes on the Lake Powell fish assemblage sampled at Wahweap (WW) nearest the dam from 1993 to 2014

Predictor variable	*df*	Likelihood ratio (*LR*) test statistics	*P*
Year	20	25.03	0.089
PC1	19	8.32	0.748
PC2	18	10.08	0.735
PC3	17	10.66	0.651

Models also included the effects of year as a covariate

not appear to influence our results because they were either too rare in captures to be considered [e.g., Rainbow Trout *Oncorhynchus mykiss* (Walbaum, 1792)], or we did not detect changes in their relative abundance over time (e.g., Striped Bass). The mechanisms responsible for the mixed response of other

Table 5 Model output from generalized additive models (GAM) for the effect of year on abiotic and biotic variables measured at the site nearest the dam, Wahweap (WW), from 1993 to 2014

Response	Predictor	*F*	*edf*	*P*	Deviance explained (%)
Water temperature	s(year)	1.11	1	0.306	5.34
Water elevation	s(year)	76.21	7.67	**< 0.001**	98.0
Phytoplankton biovolume	s(year)	20.39	4.18	**< 0.001**	85.5
Zooplankton biomass	s(year)	2.44	1.76	0.112	24.7
Nitrite + nitrate	s(year)	10.71	6.03	**< 0.001**	84.4

Significant ($\alpha = 0.05$) *P*-values are in bold

species are not immediately clear. Walleye occurred in the Colorado River prior to the formation of Lake Powell and have never been stocked into the reservoir (G. Blommer and W. Gustaveson, Utah Division of Wildlife Resources, personal communication). The observed increase in Walleye only at the GHB site is worth noting. Non-native predators, such as Walleye and Smallmouth Bass, have increased in abundance in rivers of the upper Colorado River basin (Bestgen et al., 2006; Johnson et al., 2008a, b), but it is unclear if Lake Powell is acting as a source or if individuals from smaller reservoirs in upstream watersheds of the basin are moving downstream to Lake Powell (Wolff et al., 2012).

One explanation for the increase in Walleye might be the introduction and expansion of Gizzard Shad that occurred in the early 2000s (Vatland & Budy, 2007). The timing of the increase in Walleye coincides with the first detection of Gizzard Shad at the GHB site in 2003. Gizzard Shad first entered Lake Powell from accidental introductions upstream in the San Juan River, but soon expanded and became highly abundant throughout the reservoir (Vatland & Budy, 2007). Despite only being present in fall gill net surveys since 2002, Gizzard Shad consisted of 34% of all individuals captured from 2002 to 2018. In other impounded systems, Gizzard Shad have been introduced to increase prey resources for predatory fish and are an important component of seasonal Walleye diets (Ward et al., 2007; Wuellner et al., 2010). Following Gizzard Shad introduction, Walleye catch and length-at-age increased over time in Angostura Reservoir, South Dakota (Ward et al., 2007). Although Smallmouth Bass introduced into reservoirs will also feed on Gizzard Shad (Wuellner et al., 2010), the increase in Smallmouth Bass began in the early 1990s after natural recruitment began following stocking, and prior to Gizzard Shad being introduced. The other top predator in this system, Striped Bass, which is native to the east coast USA, did not show evidence of a strong change in relative abundance over time. In Lake Powell, Striped Bass growth, consumption, condition, and abundance tend to track Threadfin Shad abundance, which dominate their diet (Vatland et al., 2008). Striped Bass can compete for food resources with other sport fishes in reservoirs (Raborn et al., 2002). Despite predictions that predator densities should decline as a reservoir ages, increasing catch rates of Walleye (at one site) and Smallmouth Bass while Striped Bass and Largemouth Bass remained relatively unchanged suggest trophic resources might not be limiting and/or some species might be subsidized by immigration from upstream rivers.

One explanation for declines in Common Carp and Channel Catfish over time is due to a trophic depression associated with reservoir aging (Miranda & Bettoli, 2010; Milbrink et al., 2011), which typically is expected to begin after the reservoir first fills (Ploskey, 1981; Turgeon et al., 2016). We did not find any statistical relationship between interannual variation in abiotic and biotic variables and fish assemblage structure at the WW site for a subset of the time series, 13 years after the reservoir first filled. Unfortunately, the lack of consistent sampling of potential abiotic and biotic variables driving changes in the fish assemblage prevented us from assessing their influence over the entire 38 years of data. Despite interannual variation, water elevation has declined, on average, since the reservoir filled in 1980. When assessing potential changes in trophic resources, it appears the prey base in Lake Powell has not undergone declines over time, and if anything, phytoplankton have increased since at least 2000, which coincides with detection of Gizzard Shad. Gizzard

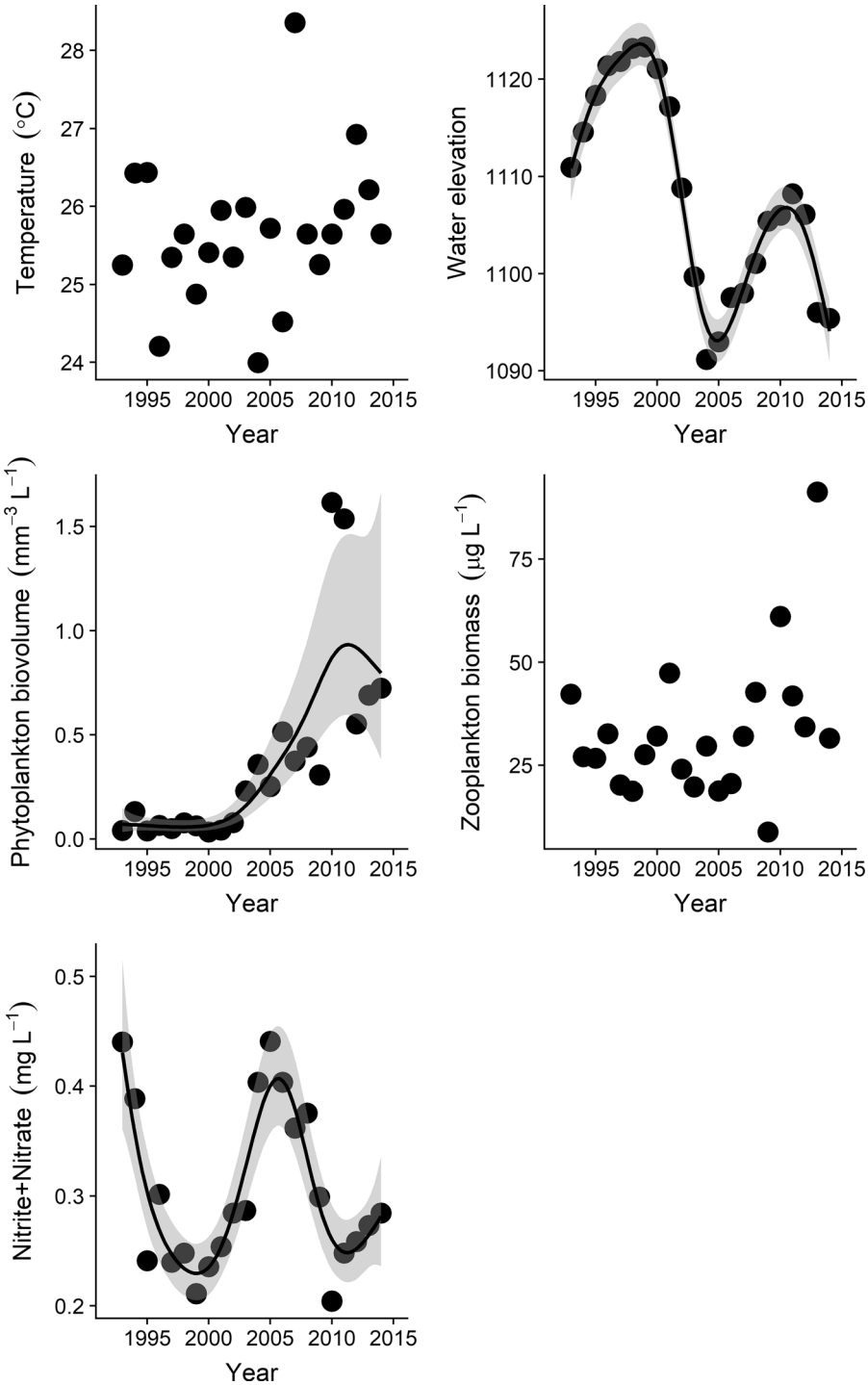

Fig. 4 Scatterplots of abiotic and biotic variables measured at the Wahweap (WW) site, nearest the dam on Lake Powell from 1993 to 2014. Trend lines and shaded areas are smoothing splines and 95% confidence intervals from generalized additive models. Variables without trend lines had non-significant ($P > 0.05$) smoothing splines. Model output is reported in Table 5

Table 6 Model output from least squares regressions testing for trends in relative weight over time for the six most abundant species

Species	*df*	Coefficient (SE)	*F*	r^2	*P*	Grand mean (range)
Channel Catfish	35	− 0.49 (0.15)	10.24	0.23	**0.003**	92 (80–137)
Common Carp	29	− 0.12 (0.08)	2.19	0.07	0.149	84 (77–93)
Largemouth Bass	35	− 0.38 (0.11)	12.14	0.26	**0.001**	96 (83–119)
Smallmouth Bass	32	− 0.51 (0.09)	31.14	0.49	**< 0.001**	85 (75–109)
Striped Bass	35	− 0.23 (0.013)	3.05	0.08	0.090	79 (65–100)
Walleye	35	− 0.21 (0.08)	7.40	0.17	**0.010**	90 (82–107)

Significant (α = 0.05) *P*-values are in bold

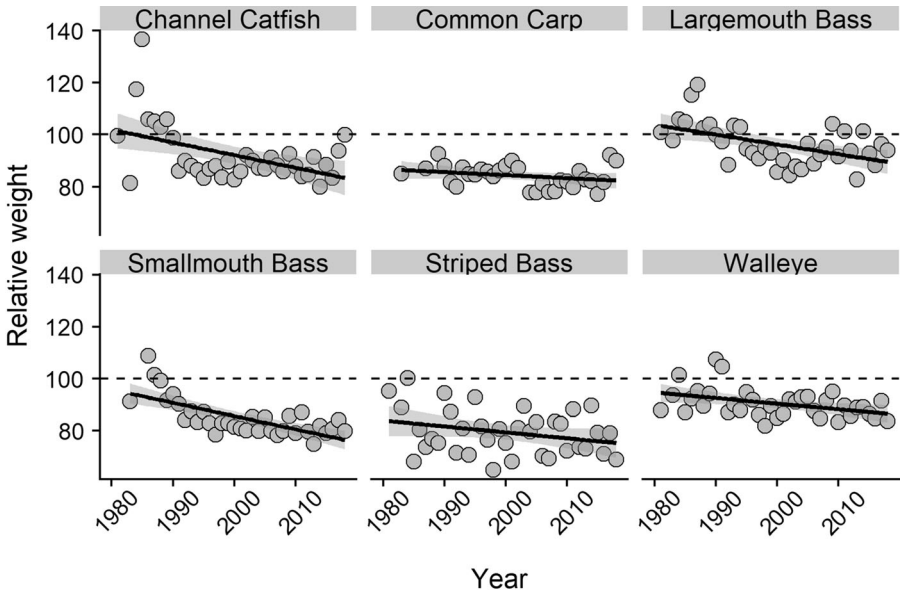

Fig. 5 Least squares regressions of relative weight over time for the six most abundant species. On average, four species showed significant ($P < 0.05$) declines in relative weight over time. Test statistics and exact *P* values are reported in Table 6. Lines are estimated means and shaded regions are 95% CI around the mean

Shad are known to stimulate phytoplankton in reservoirs through an interaction of top-down and bottom-up effects (Schaus & Vanni, 2000), and this could have implications for the food web. Zooplankton densities in Lake Powell were not obviously different between when the reservoir was first filling in the late 1960s and the late 1980s (Stanford & Ward, 1991). Zooplankton densities in the late 1960s at the downstream end of the reservoir rarely exceeded 20 individuals L^{-1} (Stanford & Ward, 1991). Average annual densities between 1993 and 2014 were similar to this value and ranged from 6.9 to 41.2 individuals L^{-1}. Plankton resources in Lake Mead, a reservoir further downstream on the Colorado River, have also not changed considerably over time (Beaver et al., 2018). Nitrite + nitrate and soluble reactive phosphorus (SRP) were inversely correlated and cycled with fluctuations in water elevation. Although interesting, none of these relatively recent patterns help explain declines in abundance of omnivorous species such as Channel Catfish and Common Carp that began in the 1980s. Low-nutrient concentrations and primary production are common in some reservoirs of the western USA (Stanford & Ward, 1991; Krogman & Miranda, 2016), but it is not clear whether this is influencing the fish community as we observed increases in predatory sport fishes, such as Walley and Smallmouth Bass, which is in contrast with the findings in more eutrophic reservoir systems (Kimmel & Groeger, 1986; Miranda & Durocher, 1986; Ploskey, 1986).

Relative weight of four species declined over time while two remained relatively constant. Of the four showing declines, Walleye and Smallmouth Bass increased in abundance over time, Largemouth Bass

remained constant, and Common Carp and Channel Catfish declined. If changes in condition were due to density dependence, we would expect condition to decline as abundance increased. However, *post hoc* correlations between relative weight and abundance were either not significant ($P > 0.05$) for Common Carp, Largemouth Bass, Smallmouth Bass, and Walleye, or were significantly positive for Channel Catfish and Striped Bass. All species had relative weights under 100, which could be driven by reduction of littoral habitat with declining water level, or relatively low productivity in Lake Powell. Lake Powell's central location within a series of reservoirs built throughout the Colorado River basin in the desert southwest likely contributes to its low productivity, low condition of these six species relative to populations throughout their range, and possibly to declines in abundance of some omnivorous species over time. Reservoirs built in series magnify the retention of sediments and nutrients leading to further oligotrophication downstream (Miranda et al., 2008; Lacerda dos Santos et al., 2018), which is linked to declines of detritivorous fishes elsewhere (Lacerda dos Santos et al., 2020). Additionally, over half the shoreline in Lake Powell consists of vertical cliffs and talus slopes with virtually no vegetation (Potter & Pattison, 1976). This, coupled with variable water levels over time could lead to declines in already limited littoral zone habitat and littoral zone productivity, which has been linked with declines in fish condition elsewhere (e.g., Milbrink et al., 2011).

Conclusions

Lake Powell experienced a re-ordering of species relative abundances driven mostly by declines in Channel Catfish and Common Carp and increases in Walleye (at one site) and Smallmouth Bass. Although we were unable to detect strong patterns of change for some species (e.g., Striped Bass), some were in relatively poor condition compared to other populations. Although invasive species, such as dreissenid mussels, can have negative impacts on aquatic food webs (Vanderploeg et al., 2002; Higgins & Vander Zanden, 2010), the timing of shifts in relative abundance of most fishes (other than maybe Walleye) we observed occurred prior to introductions of Gizzard Shad (2002) or Quagga mussels (2012). Gizzard Shad might act to slow trophic depression processes through food web stimulation (Schaus & Vanni, 2000), while Quagga mussels might act to speed them up by sequestering pelagic resources (Higgins & Vander Zanden, 2010). Reservoirs are common habitats in riverscapes of the Anthropocene that will continue to be invaded by non-native species and fill with sediments (Havel et al., 2005; Johnson et al., 2008a, b; George et al., 2017), and in the case of reservoirs in the Colorado River basin, it is likely water levels will continue to decline (Milly & Dunne, 2020). Ensuring these systems can continue to be managed for productive fisheries will require continued sampling to assess how species respond to a continually changing ecosystem. There is a need for further understanding of the mechanisms driving long-term community dynamics including how some communities are able to maintain stability in highly unstable environments, such as reservoirs, while others experience directional change (e.g., Jones et al., 2017). Classic ideas about aging processes and trophic depression might not be consistent across reservoirs from differing biomes that vary in watershed productivity and habitat complexity (e.g., Dodds et al., 2019).

Acknowledgements We thank all field crews that contributed to data collection and logistical support over the years, and W. Gustaveson and G. Blommer for allowing us access to the data. We also thank B. Healy, L. Bruckerhoff, P. Budy, C. Yackulick, and three anonymous reviewers for providing helpful comments or discussion which improved the manuscript. J. Hensleigh, B. Deemer, and C. Yackulick (USGS) helped in getting access to limnological data. The authors declare no conflict of interest. Funding was provided by the US Bureau of Reclamation (KGB and CAP).

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