

Article

Long-Term Monitoring Reveals Differential Responses of Mussel and Host Fish Communities in a Biodiversity Hotspot

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Abstract: Biodiversity hotspots can serve as protected areas that aid in species conservation. Long-term monitoring of multiple taxonomic groups within biodiversity hotspots can offer insight into factors influencing their dynamics. Mussels (Bivalvia: Unionidae) and fish are highly diverse and imperiled groups of organisms with contrasting life histories that should influence their response to ecological factors associated with local and global change. Here we use historical and contemporary fish and mussel survey data to assess fish and mussel community changes over a 33 year period (1986–2019) and relationships between mussel abundance and their host fish abundance in Bogue Chitto Creek, a tributary of the Alabama River and a biodiversity hotspot. Mussel abundance declined by ~80% and community composition shifted, with eight species previously recorded not found in 2019, and a single individual of the endangered *Pleurobema decisum*. Fish abundances increased and life history strategies in the community appeared stable and there was no apparent relationship between mussel declines and abundance of host fish. Temporal variation in the proportion of life history traits composing mussel assemblages was also indicative of the disturbances specifically affecting the mussel community. However, changes and declines in mussel assemblages in Bogue Chitto Creek cannot be firmly attributed to any specific factor or events because of gaps in historical environmental and biological data. We believe that mobility differences contributed to differential responses of fish and mussel communities to stressors including habitat degradation, recent droughts and invasive species. Overall, our work indicates that monitoring biodiversity hotspots using hydrological measurements, standardized survey methods and monitoring invasive species abundance would better identify the effects of multiple and interactive stressors that impact disparate taxonomic groups in freshwater ecosystems.



Citation: Sanchez Gonzalez, I.; Hopper, G.W.; Bucholz, J.; Atkinson, C.L. Long-Term Monitoring Reveals Differential Responses of Mussel and Host Fish Communities in a Biodiversity Hotspot. *Diversity* **2021**, *13*, 122. <https://doi.org/10.3390/d13030122>

Academic Editors: Russell Minton and Simon Blanchet

Received: 10 February 2021

Accepted: 10 March 2021

Published: 12 March 2021

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Keywords: Unionidae; life history strategies; community dynamics; host fish; stressors

1. Introduction

Climate and land use change, an increase in human population, invasive species, and direct exploitation increasingly threaten global and local biodiversity [1,2]. ‘Biodiversity hotspots’ are commonly delineated to aid in conservation strategies because they are species rich, with high levels of endemism, and are threatened by human activities [3]. Biodiversity hotspots often serve as protected areas that should prevent or mitigate the extinction of more species than protecting areas of a similar size elsewhere [3]. Typical application of the biodiversity hotspots concept through discrete biodiversity measurements can bias candidate hotspot areas exhibiting high biodiversity during initial assessments [4]. Consequently, designated biodiversity hotspots may not reflect cyclical or periodic natural disturbance regimes, or possibly obscure substantial biodiversity declines with increasing human pressures [5]. Furthermore, disparate taxonomic groups (e.g., vertebrates vs. invertebrates) may not benefit equally from protected areas [6,7]. Thus, sampling multiple taxonomic groups inhabiting designated biodiversity hotspots through time set ecological baselines, captures biodiversity trends, highlights areas of conservation concern, deter-

mines program outcomes, and can help distinguish between anthropogenic and natural disturbances influencing community turnover [8,9].

Freshwater ecosystems are inherently hotspots for biodiversity and endangerment because of the disproportionately high biological richness and human pressures relative to spatial coverage [10,11]. Delineating conservation priority areas under the biodiversity hotspot concept has been applied to freshwater systems as a primary tool for conservation with varying outcomes [12–14]. However, records of the actual effects of such protected areas on the integrity of freshwater communities are often lacking, providing no opportunity for adjustments to meet conservation goals [14]. Long-term data are fundamental to tracking the status and trends of species inhabiting biodiversity hotspots and may be especially valuable for the conservation of freshwater animals, such as mussel and fish communities [8,9].

Mussels and fish have different life histories that influence their community dynamics. Mussels are long-lived (up to >100 years), sedentary filter feeders that often occur as dense, multi-species aggregations (~10–100 individuals m⁻²) called mussel beds [15]. Mussel beds can exist in river channels that experience significant sediment mobility but can persist in the same stream locations and have similar abundance and species composition for decades [16]. In contrast, stream fish are typically shorter-lived (2–5 years), mobile animals, and their distribution and abundance are largely governed by hydrology [17]. Despite major differences in mobility, mussel and fish life history strategies can be summarized along a triangular continuum ranging from strongly r-selected to strongly K-selected that correspond to local ecological conditions [18,19]. Thus, such classification may be useful in comparing community responses of disparate taxonomic groups to ecological pressures that effect their habitats.

While major differences in mobility may influence mussel and fish community dynamics within designated biodiversity hotspots, the distribution and abundance of mussels can be linked to those of fishes. Mussels are dependent on host fish for dispersal of their ectoparasitic larval [20] and therefore can only be abundant and diverse where fish are abundant and diverse [21,22]. Because of this host–parasite relationship, fish community structure can influence mussel community structure [21,23]. However, relationships between mussel abundance and host presence are variable and dependent on-site characteristics, stability of fish populations and host specificity, among others [24]. Examining the relationship between mussel abundances and distribution of host fish is still a conservation priority [17,19] and therefore threats to mussels include threats that influence host fish populations. For example, most mussel extinction events between 1920 and 1980 were caused by impoundments and fragmentation [19,25], factors also attributed to fish population declines and extinctions [26]. Declines in freshwater mussel and fish populations have also occurred in more recent years (1980-onward), but plausible causes for fish population declines do not always explain mussel die-offs [27–29]. However, examining long-term data sets from a life history strategy perspective may offer insight into drivers of responses of co-occurring mussel and fish communities to similar pressures.

Documenting long-term community changes in designated biodiversity hotspots is key to evaluating their effectiveness as a conservation tool. Here, we used a combination of historical and contemporary data to (1) assess biological integrity and instream habitat, and quantify land use changes in the watershed to identify potential threats to freshwater communities in a biodiversity hotspot, Bogue Chitto Creek, Alabama; (2) assess fish and mussel community changes over a 33 year period (USA); (3) test whether the abundance and presence of mussels in historical and contemporary samples affect host fish community attributes. Additionally, we classified life history strategies of species using available trait data to evaluate whether suites of fish and mussel life history traits exhibit similar responses through time. Based on historically documented fish and mussel populations and suitable habitat, the Bogue Chitto Creek watershed was designated as a Strategical Habitat Unit (SHU) which entails increased focus on management and conservation. Under the assumption that this designation is meant to preserve biological and habitat diversity

associated with this area, we expected fish and mussel communities as well as habitat suitability to remain stable over time.

2. Methods

2.1. Study Area

Bogue Chitto Creek is a 937 km² watershed (Figure 1A) located in the Blackbelt Prairie Region of central Alabama and it is a tributary to the Alabama River before its confluence with the Mobile River. It provides habitat for 55 species of fish and 22 species of mussels. The lower 87 km of the Lower Bogue Chitto Creek subwatershed are designated as critical habitat by the United States Fish and Wildlife Service (USFWS) for three freshwater mussel species that historically occurred in the river: *Medionidus accutissimus*, *Hamiota perovalis* and *Pleurobema decisum* [30] (Figure 1A). Bogue Chitto Creek represents a biodiversity hotspot [3], as it was designated a strategic habitat unit by the Alabama Streams and Rivers Network (<http://www.alh2o.org/>; accessed on 8 October 2020) in 2007 because of the presence of federally and state-listed species and high biodiversity, critical habitat features needed by these species to survive, and their susceptibility to potential threats.

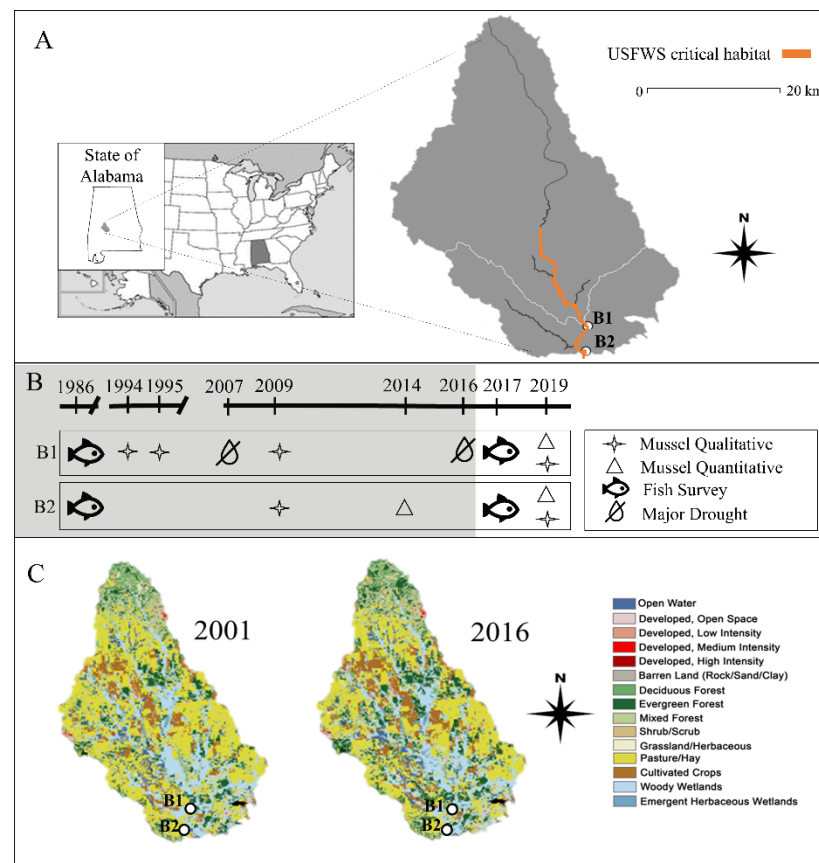


Figure 1. (A) Map of the sites sampled in Bogue Chitto Creek Watershed. (B) Timeline of the survey methodology used at each site and major drought events. Grey represents data considered historical. (C) Land cover in the Lower Bogue Chitto Creek watershed in 2001 and 2016.

The predominant land uses in the watershed are forestland and agriculture [31]. The creek also has high nutrient concentrations in comparison to other streams, as its flow-weighted total nitrogen concentration (3.90 mg/L) is within the upper 20% of 479 rivers sampled under the National Water Quality Assessment (NWQA) [32]. Additionally, Palmer Drought Severity Index (PDSI) values for the area indicate a severe drought (PDSI −3.00 to −3.99) in August 2007 [33] and an extreme drought (PDSI < −4) that occurred for multiple months of 2016 in the southeastern U.S., subsequently impacting the Bogue Chitto Creek

watershed (<https://www.ncdc.noaa.gov>; accessed on 2 May 2020). The PDSI expresses regional water availability based on the balance between water supply and environmental demand [34].

2.2. Habitat Assessment

We quantified changes in land use from 2001 to 2016 using land cover data from the National Land Cover Database (NLCD) [30] cropped to the Lower Bogue Chitto subwatershed area. Indexes of Biotic Integrity (IBI) provide information on the response of sensitive animal populations to human disturbance [35] and can be useful to assess habitat changes and to classify the biological condition of stream habitats as: “Very Poor”, “Poor”, “Fair”, “Good” or “Excellent”. We calculated IBI scores and stream biological condition based on fish survey data collected in 1986 (described below) and following O’Neal and Sheppard 2010 [36]. The biological condition of the stream in 2017 was obtained from IBI scores reported by Bearden et al. 2019 [37]. Additionally, we retrieved historical water quality data from the Water Quality Portal (<http://www.waterqualitydata.us/>; accessed on 2 May 2020) for total nitrogen (1999–2018) and conductivity (1997–2011). We recorded current water quality physical characteristics by measuring specific conductance and temperature bihourly at B1 from September 2018 to June 2020 using a submerged HOBO freshwater conductivity data logger.

2.3. Mussel Surveys

We used available historical data for mussel communities from two sites located in the Lower Bogue Chitto Creek subwatershed (Figure 1). Historical data collected by the Geological Survey of Alabama (GSA) and the Alabama Aquatic Biodiversity Center (AABC) were compiled and analyzed (Table 1). S. McGregor (GSA) sampled site B1 in 1994 and 1995 using qualitative methods and the AABC performed similar surveys at sites B1 and B2 in 2009 (Figure 1, Table 1). Briefly, untimed qualitative searches were conducted within the entire site by wading or snorkeling and finding mussels by hand. Individual mussels were identified to species and counted. The presence of invasive Asian Clams (*Corbicula fluminea*) was recorded by S. McGregor.

Table 1. Surveys conducted at B1 and B2 and the number of species recorded.

Year	Site	Type of Survey	Reference	Species Richness	Shannon’s Diversity	Combined Diversity
1986	B1 + B2	Fish Survey	GSA (Unpublished report)	33	0.69	
1994	B1	Mussel Qualitative	S. McGregor (Bearden et al. 2019)	15		
1995	B1	Mussel Qualitative	S. McGregor (Bearden et al. 2019)	14		
2009	B1/B2	Mussel Qualitative	AABC (Unpublished report)	11/12		10
2014	B2	Mussel Quantitative	AABC (Unpublished report)	10	2.07	
2017	B1 + B2	Fish Survey	GSA and ADEM (Bearden et al. 2019)	35	1.14	
2019	B1/B2	Mussel Quantitative and Qualitative	Current Study	11/7	1.90/1.24	11

Quantitative surveys were performed in 2014 and 2019. In 2014, the AABC sampled 45 quadrats at B2. In 2019, we sampled 38 and 40 quadrats at sites B1 and B2, respectively. We randomly selected four 20 m-transects along a 40–60 m reach within the mussel aggregation. We then placed 0.25 m² quadrats along each of the four 20 m transects every 2.5 m. We removed sediment to a depth of 15 cm from each quadrat and used stacked sieves to

collect mussels from all size classes. All mussels found were identified to species, counted and their longest axis was measured (i.e., length [mm]). The abundance of the invasive clam, *C. fluminea*, was also recorded at each quadrat in 2019. Quantitative surveys with substrate sieving provide a more accurate representation of density and abundance [38] while qualitative surveys or timed searches provide a more complete species list [39]. We performed additional timed searches in 2019 following quantitative efforts to obtain a comprehensive sample of the mussel species composition. We considered all data prior to the 2019 surveys as historical data (Figure 1).

2.4. Fish Collection and Assignment as Hosts

We used fish community data collected by GSA and the Alabama Department of Environmental Management (ADEM) in 1986 and 2017 (prior to and following the two major regional droughts) within our study reaches to evaluate host fish availability and IBI. Sampling combined seining and backpack electrofishing following the methodology of the Index of Biologic Integrity in the Hills and Coastal Terraces Ichthyoregion in Alabama [35]. Briefly, surveyors performed a minimum of 10 sampling efforts at each distinct type of habitat; riffle, pool, run or shoreline, and at least 32 efforts at the site [36].

We determined host suitability of surveyed fish using the Freshwater Mussel Host Database [40] for each recorded mussel species in Bogue Chitto Creek in historical and contemporary samples. Fish classified as host with evidence of “natural transformation”, “natural infestation” or “lab transformation” were deemed to be suitable host fish species for the purposes of our study.

2.5. Mussel and Fish Life History Strategy Classifications

We used the life history strategy classification for mussels based on Haag (2012) [19] to divide mussel species in Bogue Chitto Creek in the three life history strategies (Table S1). This classification is based on maximum life span (years), age at maturity (years), and fecundity (number of glochidia) or growth rate (K).

We used scientific literature and electronic databases [41,42] to comprehensively describe fish life history strategies in Bogue Chitto Creek (Table S2). Fish life history traits included life span (years), age at maturity (years), fecundity (total number of eggs or offspring per breeding season), and egg size (mean diameter [mm]). Additionally, we adopted methods from Winemiller (1989) [43] to calculate parental investment, a metric representing the total energetic contribution of parents to their offspring. Next, we assigned fish life history strategy endpoints and evaluated the fish life history continuum model of Winemiller and Rose [18] by plotting species' positions in relation to three life history axes: (1) \log_{10} maturation age; (2) \log_{10} fecundity; and (3) \log_{10} investment per progeny (calculated as \log [egg diameter + parental care]; Figure S1). The equilibrium strategy is usually characterized by high parental care, low fecundity and low maturation while the opportunistic is associated with early maturation, low parental care and low fecundity. The periodic strategy is intermediate and is related to high fecundity, low parental care and late maturation [18,19]. Following life history classification assignment for mussels and fish, we calculated the proportion of species with each strategy for each time period and assessed temporal changes in each community simultaneously using a ternary diagram. Because qualitative mussel surveys were performed during all time points, we felt estimated species richness and therefore associated life history strategy composition, were accurately represented.

2.6. Statistical Analyses

We used traditional biodiversity metrics including richness, abundance and Shannon's diversity index for each site and time period for mussel and fish communities. We calculated the combined diversity for all the mussel assemblages surveyed for each sampling period to examine diversity patterns for the stream. We used quantitative surveys to evaluate changes in Shannon's Diversity between 2014 and 2019 while we added qualita-

tive surveys when comparing species richness, relative abundance and presence/absence across all years. We only compared total abundance between similar sampling techniques: qualitative samples at site B1 in 1994, 1995, 2009 and 2019 and quantitative samples at B2 in 2014 and 2019. We used one-way ANOVA to analyze statistical differences in Shannon's diversity and we analyzed spatial differences in mussel density between sites B1 and B2 using Wilcoxon test as the data did not follow a normal distribution.

We quantified changes in fish abundance and species richness between 1986 and 2017. Additionally, we tested the relationship between host fish and mussel abundance from combined results of qualitative and quantitative efforts in the Bogue Chitto Creek in 1994 and 2019 and the number of available host fish abundance, host fish species and host fish families in 1986 and 2017, respectively. We performed analysis of covariance (ANCOVA) to determine whether the relationship between host species or host family abundance and mussel abundance differed between two sampling periods, historical (1986/1994) and contemporary (2017/2019). Mussel abundance data were \log_{10} transformed to meet assumptions of normality and heterogeneity.

3. Results

3.1. Habitat Changes

Land cover in the Lower Bogue Chitto Creek subwatershed did not change drastically between 2001 and 2016 (Figure 1C). There was an increase in developed areas (+0.9%) and cultivated crops (+2.5%) while the dominating land use, hay, decreased (−8.76%) (Table 2). However, IBI indicated instream habitat considerably changed. The biological condition of the stream decreased from “fair” in 1986 (IBI score 38) to “poor” in 2019 (IBI score 32). Historical total nitrogen ranged from 0.19 to 1.31 mg/L and was on average 0.60 ± 0.038 while yearly averages ranged from 0.51 to 0.74 mg/L. Historical conductivity ranged from 101 to 211 $\mu\text{S}/\text{cm}$ and was on average $156.7 \mu\text{S}/\text{cm} \pm 2.66$. Conductivity measured in the stream between September 2018 and June 2020 ranged from 20.84 $\mu\text{S}/\text{cm}$ in June to 799 $\mu\text{S}/\text{cm}$ in early October and was on average $240 \pm \mu\text{S}/\text{cm}$ (Figure S2).

Table 2. Land use percentages from 2001 to 2016.

Year	Land Cover	Open Water	Developed	Deciduous Forest	Evergreen Forest	Mixed Forest	Crops	Hay	Woody Wetlands	Emergent Herbaceous
2001		3.08	0.79	3.99	9.89	10.02	8.48	42.76	18.31	2.67
2004		3.64	1.60	4.00	11.12	10.26	8.68	39.65	17.34	3.70
2006		3.59	1.62	3.95	12.34	10.32	9.00	38.28	18.14	2.76
2008		3.59	1.65	3.66	12.81	10.08	9.56	37.56	17.88	3.20
2011		3.59	1.68	3.59	13.42	10.09	10.12	36.17	17.53	3.82
2013		3.51	1.67	3.81	13.91	10.42	10.17	35.53	18.28	2.71
2016		3.25	1.69	3.71	13.87	10.57	10.98	34.77	18.32	2.84

3.2. Mussel Abundance

We found 174 mussels during the first qualitative surveys performed at site B1 in 1994. In 2009, mussel abundances declined by 33% to 118 individuals. Mussel abundance declined by 68% at site B1 between 2009 and 2019, when only 38 mussels were found combining both qualitative and quantitative methods. Total abundances at site B2 decreased from 39 to six between quantitative surveys in 2014 and 2019, which represent an 85% loss in the number of mussels. Mussel lengths ranged from 14 to 98 mm and were 52.9 ± 2.24 on average. In 2019, the mean mussel density at B1 was 1.23 ± 1.86 mussels m^{-2} and was significantly greater ($T_{(38)} = -2.31$ $p = 0.021$) than density at B2, which was 0.5 ± 0.2 mussels m^{-2} . The invasive Asian clam, *C. fluminea*, was recorded in 1994/1995 surveys and was largely present at both sites in 2019. *Corbicula fluminea* densities at site B1 were 2.1 individuals m^{-2} and 6.40 individuals m^{-2} at B2 (Table 3).

Table 3. Proportional abundance of mussel species from qualitative surveys performed in 1994, 1995 and 2009 and mean densities and total abundance from quantitative surveys performed in 2014 and 2019 for two sites in Bogue Chitto Creek. Species conservation status is indicated by superscripted letter following name (Alabama Department of Wildlife and Fisheries). * *C. fluminea* not computed for relative unionid abundance. ** Indicates that additional qualitative surveys were performed (Table S3). ^E Indicates that the species is federally endangered.

B1	1994	1995	2009	2014		2019			
Species	Proportional Unionid Abundance (%)	Proportional Unionid Abundance (%)	Proportional Unionid Abundance (%)	Abundance	Proportional Unionid Abundance (%)	Mean Density (mussels/m ²)	Abundance	Proportional Unionid Abundance (%)	Mean Density (mussels/m ²)
<i>Amblema plicata</i>	86.20	45.04	22.68				8	38.1	0.84
<i>Corbicula fluminea</i> *	NA	NA	NA				20	NA	2.12
<i>Cyclonaias asperata</i>	0.57	0.90	41.17				6	28.5	0.60
<i>Fusconaia cerina</i>	0	0	0.85				0	0	0
<i>Leptodea fragilis</i>	0.57	0.90	0.85				1	3.2	0.10
<i>Lampsilis ornata</i>	0.57	0	0.85				1	3.2	0.10
<i>Lampsilis teres</i>	2.29	0.90	0.85				0	0	0
<i>Obliquaria reflexa</i>	0.57	0.90	5.04				2	6.4	0.21
<i>Pleurobema decisum</i> ^E	1.14	0.90	1.68				0	0	0
<i>Potamilus purpuratus</i>	2.29	45.04	3.36				0	0	0
<i>Pyganodon grandis</i>	0.57	0.90	0.84				0	0	0
<i>Quadrula apiculata</i>	1.14	0.90	13.44				2	6.4	0.21
<i>Tritogonia verrucosa</i>	1.14	0.90	3.36				0	0	0
<i>Toxolasma parvum</i>	0	0	0				1	3.2	0.10
<i>Villosa lienosa</i>	1.14	0.90	1.68				0	0	0
Total unionids	174	110	118				21 **		
B2									
<i>Corbicula fluminea</i>			NA	NA	NA	NA	64	NA	6.40
<i>Cyclonaias asperata</i>			2	8	20.51	0.72	3	50	0.30
<i>Fusconaia cerina</i>			0	1	2.56	0.08	0	0	0
<i>Lampsilis ornata</i>			0	2	5.12	0.16	0	0	0
<i>Lampsilis straminea</i>			8	0	0	0	0	0	0
<i>Lampsilis teres</i>			4	5	12.82	0.44	0	0	0
<i>Lasmigona alabamensis</i>			6	0	0	0	0	0	0
<i>Leptodea fragilis</i>			2	4	10.25	0.32	0	0	0
<i>Medionidus accutissimus</i>			2	0	0	0	0	0	0
<i>Megalonaias nervosa</i>			48	2	5.12	0.16	0	0	0
<i>Obliquaria reflexa</i>			0	0	0	0	1	16	0.10
<i>Pleurobema decisum</i> ^E			NA	5	12.82	0.44	0	0	0
<i>Potamilus purpuratus</i>			2	0	0	0	0	0	0
<i>Pyganodon grandis</i>			2	0	0	0	0	0	0
<i>Quadrula apiculata</i>			2	1	2.54	0.08	0	0	0
<i>Toxolasma parvum</i>			0	0	0	0	1	16	0.10
<i>Tritogonia verrucosa</i>			2	0	0	0	0	0	0
<i>Truncilla donaciformis</i>			2	2	5.12	0.16	0	0	0
<i>Villosa lienosa</i>			0	9	23.08	0.8	1	16	0.10
Total unionids			50	39			6 **		

3.3. Mussel Richness and Assemblage Composition

A total of 20 species, including three endangered species (*H. perovalis*, *M. accutissimus* and *P. decisum*) were documented in 1994 and 1995 (McGregor 1994, Table 1). The number of species at site B1 in 1994 and 1995 was 15 and 14, respectively. Richness decreased to 11 at B1 and none of the threatened or endangered species was found during quantitative efforts in 2019. A similar trend was observed at B2. A total of 12 and 10 species were recorded in 2009 and 2014, respectively, while only seven species were recorded in 2019 (including the mussels found during the additional timed searches; Table S3). We did not have historical data to calculate Shannon's diversity at B1, but Shannon's diversity decreased at site B2 from 1.90 in 2014 to 1.24 in 2019. The overall richness and Shannon's diversity were greater at B1 than at B2. However, Shannon's diversity was not significantly different among the three quantitative surveys ($F_{(23)} = 2.63$, $p = 0.09$).

Species dominance and relative abundances varied across time and sample events. While *Cyclonaias asperata* was dominant in the quantitative surveys performed in 2009 at site B1, the most abundant unionid species in 2019 was *Amblema plicata* (Table 3). A similar case occurred at site B2 where *Megaloniaias nervosa* was the most abundant species in 2009 but decreased to two individuals in 2014 and was not found during the 2019 survey. *Cyclonaias asperata* was the dominant species at site B2 in 2019 (Table 3).

3.4. Fish Communities and Host–Mussel Relationships

In the 1986 surveys, 283 fishes from 32 different species belonging to five families were collected. In 2017, both richness (35 species recorded) and abundance (565 individuals) increased. Shannon's diversity varied from 0.69 in 1986 to 1.14 in 2017. While fish richness remained stable, species turnover was high, with 11 of the species recorded in 1986 not found in 2017 (Table S3). We identified nine species as suitable mussel hosts (Table 4). Suitable host fish of *Amblema plicata* had the greatest abundance in 1986 and 2017. The ANCOVA revealed that there was a positive relationship, between the number of host fish species in relation to mussel abundance ($F_{3,15} = 4.64$, $R^2 = 0.37$, $p = 0.02$). This relationship was mainly driven by the high abundance of *Amblema plicata* in 1994 (150 individuals) and fell apart when we removed this species from the analysis ($F_{3,14} = 1.057$, $R^2 = 0.009$, $p = 0.40$). We found no significant relationships between the number of host fish families ($F_{3,15} = 2.37$, $R^2 = 0.19$, $p = 0.19$) or host fish abundance (Figure 2; $F_{3,15} = 2.42$, $R^2 = 0.19$, $p = 0.106$) with mussel abundance.

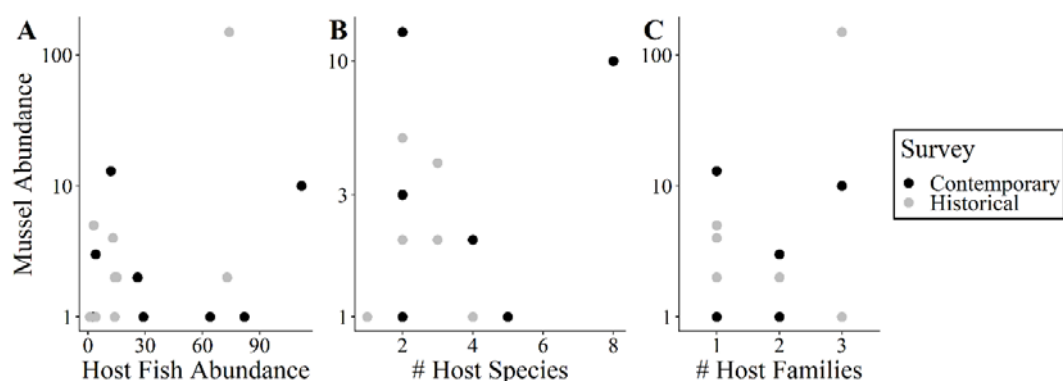


Figure 2. Host fish and mussel abundance relationships for 1986 and 1994 (historical data), respectively, and for 2017 and 2019 (contemporary data). The y axis is log₁₀ transformed for visualization and data analysis. (A) Host fish abundance and relation to mussel abundance ($F_{3,10} = 5.72$, $R^2 = 0.520$, $p = 0.01$). (B) Number (#) of host fish species and mussel abundance ($F_{3,14} = 1.057$, $R^2 = 0.009$, $p = 0.40$); abundance of *Amblema plicata* was removed for analysis and visualization. (C) Number (#) of host fish families and mussel abundance ($F_{3,10} = 2.02$, $R^2 = 0.19$, $p = 0.17$).

Table 4. Previously recorded (GSA/ADEM) number (#) of fish species and families and total abundance of fish that serve as host for freshwater mussels found in Bogue Chitto Creek surveys in 2019. ¹ Indicates mussel species present only in 1994. ² Host fish species were not present in Bogue Chitto surveys. ³ Indicates fish were only present in 2017 surveys.

Mussel Species	Host Fish Species	Host Fish Family	# Host Fish Species		# Host Fish Family		Host Fish Abundance	
			1986	2017	1986	2017	1986	2017
<i>Amblema plicata</i>	<i>Cyprinella venusta</i> , <i>Lepomis cyanellus</i> , <i>L. gulosus</i> , <i>L. megalotis</i> , <i>L. macrochirus</i> , <i>Micropterus salmoides</i> , <i>Moxostoma erythrum</i> , <i>Percina caprodes</i> , <i>Pomoxis nigromaculatus</i>	Centrarchidae, Percidae, Cyprinidae, Catostomidae	5	9	3	4	74	112
<i>Cyclonaias asperata</i>	<i>Ictalurus punctuatus</i> , <i>Noturus leptacanthus</i>	Ictaluridae	1	2	1	1	3	12
<i>Lasmigona alabamensis</i>	Unknown							
<i>Leptodea fragilis</i>	<i>Aplodinotus grunniens</i> ²							
<i>Lampsilis ornata</i>	<i>M. salmoides</i>	Centrarchidae	1	1	1	1	1	3
<i>Lampsilis teres</i>	<i>L. cyanellus</i> , <i>L. gulosus</i> , <i>L. macrochirus</i> , <i>L. megalotis</i> , <i>M. salmoides</i> , <i>P. nigromaculatus</i>	Centrarchidae	3	6	1	1	13	29
<i>Obliquaria reflexa</i>	<i>L. chrysocephalus</i> , <i>M. salmoides</i>	Centrarchidae, Cyprinidae	2	2	2	2	14	4
<i>Pleurobema decisum</i>	<i>C. venusta</i> , <i>L. chrysocephalus</i>	Centrarchidae	2		1		73	82
<i>Quadrula apiculata</i>	Unknown							
<i>Toxolasma parvum</i>	<i>Etheostoma nigrum</i> , <i>L. cyanellus</i> , <i>L. gulosus</i> , <i>L. macrochirus</i>	Centrarchidae, Percidae	2	4	1	1	5	26
<i>Villosa lienosa</i>	<i>L. cyanellus</i> , <i>L. megalotis</i> , <i>M. salmoides</i> , <i>I. punctuatus</i>	Centrarchidae, Ictaluridae	3	4	2	2	15	64
<i>Hamiota perovalis</i> ¹	<i>Micropterus salmoides</i>	Centrarchidae	1		1		1	
<i>Pyganodon grandis</i> ¹	<i>L. macrochirus</i> , <i>M. salmoides</i> , <i>Dorosoma cepedianum</i> , <i>Ameiurus natalis</i> , <i>P. nigromaculatus</i>	Centrarchidae, Clupeidae, Ictaluridae	4		3		4	
<i>Potamilus purpuratus</i> ¹	<i>Lepomis cyanellus</i> ³ , <i>Aplodinotus grunniens</i> ²	Centrarchidae						
<i>Tritogonia verrucosa</i> ¹	<i>Lepomis gulosus</i> ³ , <i>A. natalis</i> , <i>I. punctuatus</i> , <i>G. affinis</i> , <i>N. texanus</i> ³	Ictaluridae, Poeciliidae	2		2		14	
Total Number			10	14	4	5		

The total number of available host species, families and individuals increased in 2017 (Table 4). We identified 14 species belonging to five different families as hosts for the mussels found in 2019 from the fish recorded in 2017. Host abundance increased from 93 in 1986 to 179 individuals in 2017 (Table 4). *Amblema plicata* had the most available host species and families (Table 4).

3.5. Temporal Shifts in Life History Strategies

The percentage of different mussel life history strategies in Bogue Chitto Creek varied among sampling events. While equilibrium life history strategies remained dominant between 1994 and 2019, representing a 91% and 76% of the community, respectively, periodic strategist species increased from representing 1% to 14% (Figure 3). Opportunistic species represented a small part of the community throughout all sampling periods.

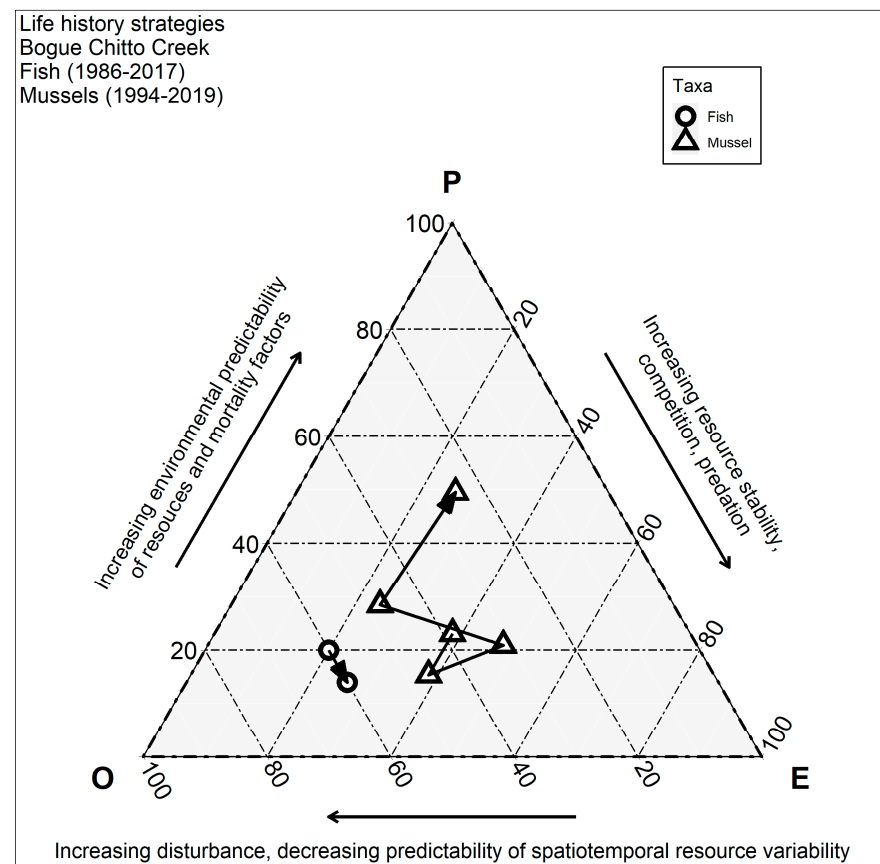


Figure 3. Exploratory visualization of temporal variation in the proportion of species within the three life history strategies (E = equilibrium, O = opportunistic, and P = periodic) of fish and mussels in Bogue Chitto Creek.

Changes in the fish life history community composition were minimal (Figure 3). The community was clearly dominated by fish within opportunistic life strategies which represented 86% and 81% of the fish sampled in 1986 and 2017, respectively. However, equilibrium species slightly increased from 6% to 16% while periodic decreased from 7% to 2%.

4. Discussion

Aquatic communities can shift over time due to anthropogenic activities and natural variation [44,45], but whether co-occurring taxonomic groups respond similarly through time is rarely evaluated. We demonstrated divergent responses of two taxonomic groups, fish and mussels, over a period of approximately 30 years, in a freshwater diversity hotspot

and area of high conservation concern. Mussel abundances were not related to host fish communities, indicating that mussel populations are decreasing despite host availability. Overall, changes in habitat suitability, represented by instream habitat degradation and environmental flow disruptions caused by extreme droughts, in this area in 2007 and 2016 may have impacted mussels more than fishes. We attribute this to the difference in mobility in these two groups. Specifically, the conditions in our system appear to be especially harmful to sedentary, long-lived organisms as we saw abundance declines and changes in life history strategies in freshwater mussel assemblages, but not in co-occurring fish communities.

In contrast to our expectations based on the biodiversity hotspot concept, population stability relative to their historical condition was different among fish and mussels. Mussel communities were degraded while fish communities were stable through time. Despite having only two time points for fish data, mussel (24 years) and fish (31 years) covered similar time spans. Yet, our ability to discern whether the contemporary fish community is within the range of conditions that reflect expected variation or has moved beyond previous bounds (pre-1986) in response to environmental change is limited. Overall, we cannot state that the fish populations did not change between 1986 and 2017, but that they appeared stable when comparing both sampling points.

Mussel abundance in Bogue Chitto Creek has experienced alarming declines based on our comparison between historical and contemporary surveys, with mussel populations reduced by almost 80%. Fish communities did not follow the same pattern and almost doubled in number when comparing historical and contemporary data. Importantly, three habitat-tolerant species, *Notropis stilbius*, *Lepomis megalotis*, and *Gambusia affinis*, drove the increase in abundance. Additionally, mussel richness decreased at both sites while fish richness and diversity increased since 1986. Eight mussel species previously recorded were not found in 2019 (Table 3) and it is important to highlight that Bogue Chitto Creek is a USFWS-designated critical habitat for three of those species: *M. acutissimus*, *H. perovalis* and *P. decisum*. Although we did not find *P. decisum* during the quantitative surveys in 2019, we found one individual during additional time searches at site B2, indicating a potential low presence of this species. The larger sized individuals and low population densities of mussels also show the low recruitment activity occurring in Bogue Chitto Creek. However, smaller individuals (~14 mm) of three species were collected during the survey.

Changes in host fish community composition could also lead to declines in freshwater mussels [22]. However, we found no significant relationships between host fish and mussel abundances. Families and number of hosts increased from 1986 to 2017 except for one of the hosts for *Obliquaria reflexa*, *Luxilus chrysocephalus*, which declined from 13 to one individual. The increase in host fish populations was mostly attributable to the increase in *Lepomis* species that serve as host for four of the mussel species recorded. Overall, the increase in host fish, and the lack of relationships between mussels and fish communities suggest that factors affecting mussel declines were independent of host fish persistence. However, our understanding of fish–mussel relationships is still limited as the host fish for several species remain unidentified [19].

Despite the lack of relationships between host fish abundance and freshwater mussels, we evaluated habitat characteristics that could be potentially affecting both populations. Landcover analyses and the IBI scores indicated that both watershed land use and in-stream habitat condition has declined in the watershed. While land use did not considerably change from 2001 to 2016 and total nitrogen concentrations remained stable over time, there was an increase in anthropogenic land uses such as cultivated crops and development, and although hay land cover declined, it is still the primary land use in the watershed (Table 2). Agriculture and urban areas can be main contributors to run-off increasing nutrient concentrations and sediment [46], creating favorable habitat for pollution-tolerant species. Additionally, aquaculture is one of the main economic activities in the watershed as Dallas and Perry counties combine for 10 farms and 36 Channel catfish (*Ictalurus punctuatus*) ponds [47]. Ponds are treated annually in late summer or early autumn with

Sodium Chloride (NaCl) and may increase natural stream salt concentrations through effluent inputs or accidental spills [48,49]. Data collected in 2019 show peak stream-specific conductance values of 799 $\mu\text{s}/\text{cm}$ in late September and early October, coinciding with low flows in the stream and salt application times of catfish ponds. Although the value is still under the normally accepted limit for freshwater organisms of 1000 $\mu\text{s}/\text{cm}$ [50], the variation from the measured average conductance of 240 $\mu\text{s}/\text{cm}$ in the stream and baseline concentrations is substantial. The recorded concentrations also differ from historical data (1999–2018) that was on average 156.7 $\mu\text{s}/\text{cm}$. Fishes inhabiting Bogue Chitto Creek might find refuge from such disturbances by moving into tributaries or downstream, while sedentary mussels would be unable to escape this high stress event.

The introduction of non-native species may be another factor contributing to habitat degradation in this system. Introduced Asian Clams, *C. fluminea*, may have adverse effects on native mussel populations through direct competition [28,51]. *Corbicula fluminea* densities in Bogue Chitto Creek were three times higher than the most abundant native mussel species. Although the presence of *C. fluminea* was recorded for the first time in Bogue Chitto Creek in 1984 [52], detailed historical accounts of *C. fluminea* populations are not readily available and it is still not common to measure or record data on their populations as it is time intensive. However, recording abundances of invasive species such as *C. fluminea* may provide useful information to make population estimates and document invasion rates and understand their effects on native species [53].

When evaluating habitat suitability in a watershed, land use and resulting water quality and instream flows are just as important. Flow stability in particular may be critically important for sedentary groups such as mussels that cannot move rapidly away from desiccation as a result of extreme low-flow events [54]. The interaction of instream habitat degradation and extreme droughts [55] could be especially damaging to sedentary organisms such as freshwater mussels. Two major drought events occurred in the watershed within the last 15 years (Palmer Drought Hydrological Index -4 and below). The 2016 drought represented the second driest October in Alabama since 1895 [56]. Broad life history of strategies of fish and mussels allowed us insight on how their community composition changed over time. Based on contemporary data mussel assemblage composition shifted from a more equilibrium and opportunistic strategists to more periodic species. In contrast, life history strategies within the fish community remained much more stable, mostly comprising opportunistic species (Figure 3). Although fauna-wide declines in mussel populations hinder our ability to attribute changes in relative abundance to life history strategies, the increase in periodic species could be associated with behavioral and physiological adaptations for the species in this group. For example, periodic strategists may have been better adapted to survive recent drought because they have the highest mobility and intermediate tolerance to desiccation [57]. Due to the dynamic nature of river ecosystems and data limitations, we cannot rule out the possibility that mussel beds are forming in other reaches of Bogue Chitto Creek or report on the stability of other mussel populations in the region that may have been affected by drought-induced stream drying. Previous studies have found that mussel beds are persistent over long periods of time [58] but can be restructured by stream drying events [16,59]. Increasing frequency and intensity of stream drying events expected with global change may transform rivers such as Bogue Chitto Creek to favor assemblages with different suites of life history traits.

5. Conclusions

Our study shows substantial differences in the vulnerability of two distinct taxonomic groups which we hypothesize is attributed to differences in mobility. Monitoring changes in co-occurring fish and mussel communities allows us to understand how stressors in the watershed can disproportionately influence different organisms. Habitat degradation, changing climate and unprecedented rates of species invasions could all be contributing factors to the disappearance of mussel assemblages in the watershed. Declines in mussel species richness and habitat quality (fish IBI) across the 33 year timeframe should be

alarming. The relative stability of fish abundances and the lack of an observable relationship between mussels and abundance of host fish could indicate that flow cessation during droughts with the interaction of other contributing stressors is especially impacting mussels due to their lack of mobility. Additionally, long life spans and slow recovery rates of mussels compared to the shorter live opportunistic fish species that appear resilient to stressors impacting Bogue Chitto Creek may contribute to the pattern observed here. Enigmatic mussel declines have been occurring in the U.S since 1960 [28]. However, our knowledge of freshwater mussels, including life history strategies and adaptations, and fish host–mussel relationships is still limited. Freshwater mussels are understudied and often excluded from conservation planning, resulting in data limitation that prevents proper assessments of mussel population status [60] and causal explanations of changes in mussel community structure. It is important to monitor biodiversity hotspots such as Bogue Chitto Creek using standardized survey methods at regular and meaningful time points to understand aquatic animal community dynamics. Determining the impact of multiple stressors on different taxonomic groups is essential to species conservation and to evaluating the effectiveness of biodiversity hotspots as conservation tools.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/3/122/s1>, Figure S1: Three-dimensional plot of \log_{10} (maturation age), \log_{10} (fecundity), and relative investment per progeny ($\log_{10}(\text{egg diameter} + \text{parental care} + 1)$) for the fishes of the Bogue Chitto Creek according to the trilateral continuum model of fish life histories (Winemiller and Rose 1992). All species for both sampling periods (1986 and 2017) are plotted and grouped by family because nonmajor shifts in strategies were observed. Figure S2: Temperature (blue line) and conductivity (orange line) at Bogue Chitto Creek site B1 from September 2018 to June 2020. Table S1: Freshwater mussel life history strategies assigned following Haag (2012). Table S2: Fish species, abundance, and life history strategies found in 1986 and 2017 surveys. Table S3: Species and individuals found in additional mussel qualitative surveys in 2019.

Author Contributions: Conceptualization, I.S.G., G.W.H. and C.L.A.; Methodology, I.S.G., G.W.H. and C.L.A.; Formal Analysis, I.S.G.; Investigation, I.S.G., G.W.H., J.B. and C.L.A.; Data Curation, I.S.G.; Writing—Original Draft Preparation, I.S.G.; Writing—Review and Editing, I.S.G., G.W.H., J.B. and C.L.A.; Visualization, I.S.G., G.W.H. and C.L.A.; Supervision, C.L.A.; Project Administration, C.L.A.; Funding Acquisition, C.L.A. All authors have read and agreed to the published version of the manuscript.

Funding: Funding for this project was provided by National Science Foundation DEB-1831512.

Institutional Review Board Statement: Freshwater mussels are invertebrate animals and not governed by the Institutional Animal Care and Use Committees (IACUC).

Informed Consent Statement: Not applicable.

Data Availability Statement: Data is reported in tables throughout the article and held with C.L.A. and I.S.G.

Acknowledgments: We thank Ansley Hamid, Austin Beets and Michael Buntin for assistance in fieldwork. Megan Kubala, Matt Lodato, Ariel Shogren and Brian van Ee provided useful suggestions on earlier versions of the manuscript. Nate Jones helped with land use data analysis. Historical data was provided by the Alabama Aquatic Biodiversity Center, Geological Survey of Alabama and the Alabama Department of Environmental Management. We also thank Stuart McGregor for providing notes and clarification regarding historical data collection. The Weyerhaeuser Company and National Science Foundation DEB-1831512 and DEB-1942707 provided support for this project. Freshwater mussel collection was conducted under USFWS permit #TE68616B-1 and ALCDNR permit #2016077745468680.

Conflicts of Interest: The authors declare no conflict of interest.

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