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Response of freshwater mussel assemblages (Bivalvia:Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia

STEPHEN W. GOLLADAY[1], PAULA GAGNON[2], MARGARET KEARNS[3], JULIANN M. BATTLE[4], AND DAVID W. HICKS[5]

J. W. Jones Ecological Research Center, Route 2, Box 2324, Newton, Georgia 39870 USA

Abstract. Freshwater mussel assemblages in the Flint River Basin (FRB) of southwestern Georgia are among the most diverse in the southeastern Coastal Plain of North America. Historically, 29 species, including 7 endemics, occurred in the FRB. A drought during the summer of 2000 caused record low flows and many perennial streams dried or became intermittent. Predrought surveys conducted in 1999 allowed an assessment of the impact of the drought on mussel assemblages. During 2001, 21 stream reaches that had abundant or diverse mussel assemblages in 1999 were resurveyed. Study sites were classified as flowing or non-flowing during the drought based on data from stream gauging stations or visual observation of study reaches. Mussels were classified by conservation status, either stable, special concern, or federally endangered. Greater than 90% of the mussels observed in the lower FRB were species with stable conservation status. Special-concern species represented 5 to 6% and endangered species represented 1% of mussel abundance. Sites that ceased flowing during the drought had significant declines in the abundance of stable species and in taxa richness. Endangered species also showed evidence of a decline in non-flowing sites. Sites that maintained flow had increases in stable species and no change in special concern, endangered species, or species richness through the drought. Sites that showed declines in mussel abundance had a significantly lower frequency of wood debris than other sites. Field observations suggested that shallow depressions beneath wood debris may act as refuges for freshwater mussels during stream drying. Greatest declines in mussel abundance usually occurred in the mid-reaches of the major tributaries of the lower Flint River. These reaches depend on the Upper Floridan aquifer, which is heavily used for irrigation, to maintain base flows. Declines in mussel populations appear to be associated with unusual climatic conditions and increasing demand on the area streams and the regional aquifer system for irrigation water supply.

Key words: freshwater mussels, Unionidae, endangered species, drought, Flint River, hydrology, climate change impacts, wood debris.

Freshwater mussel assemblages in the Flint River Basin (FRB) of southwestern Georgia are among the most diverse in the southeastern Coastal Plain of North America. Historically, 29 species of mussels, 7 of which were endemic, occurred in the FRB (Clench and Turner 1956). Surveys conducted between 1991 and 1993 found that several Flint River tributaries within the Coastal Plain (lower FRB) continued to harbor a diverse mussel fauna, ranging from 9 to 16 species, including several endangered species (Brim Box and Williams 2000). However, only 22 of the 29 species originally found in the FRB were observed during the 1991 to 1993 survey (Brim Box and Williams 2000). The tributary streams of the lower FRB were the area where the highest concentration of endangered species occurred, and the most abundant and diverse communities were noted.

A prolonged drought occurred from 1999 through 2002 in southwestern Georgia. The most severe part of the drought occurred during the summer of 2000 when many perennial streams dried. In some locations, headwater sections sustained flow, while downstream sections dried (Johnson et al. 2001). In other locations, mostly larger streams, flowing water persisted throughout the drought; however, water levels dropped to unprecedented lows (USGS 2000).

The drought had widespread impact on streams supporting mussel populations across the lower FRB. Predrought population surveys conducted in 1999 provided baseline information to assess drought impacts (Johnson 2001). In addition, previous studies in the lower FRB suggested that wood debris may offer refuges

[1] E-mail addresses: sgollada@jonesctr.org
[2] jmaluap@yahoo.com
[3] margaret.kearns@state.ma.us
[4] jbattle@stroudcenter.org
[5] whicks@jonesctr.org

for mussels during stream drying (Johnson 2001, Johnson et al. 2001). The purpose of our study was to conduct additional field surveys to assess the regional extent of mussel population losses during the 2000 drought and determine whether mussel survival was associated with the abundance of wood debris. Specific objectives included 1) determining the extent and nature of change in mussel assemblages as a result of drought conditions experienced during summer 2000, 2) identifying stream reaches that were most adversely impacted by drought, 3) determining the impact of stream drying on mussel assemblages, and 4) determining whether mussel survivorship was associated with the abundance of wood debris in stream reaches.

Methods

Study site

Our study was done in tributary streams of the lower FRB (Fig. 1), on the Coastal Plain physiographic province of southwestern Georgia. Many of the streams originate as seeps and springs emanating from the Claiborne aquifer in the Fall Line Hills physiographic district. The streams flow onto the Dougherty Plain district downstream where low topographic relief in combination with porous surface geology results in low stream drainage density and a dominance of subsurface water flow (Hicks et al. 1987). Major streams and their tributaries have channels incised within the Upper Floridan aquifer and are perennial during normal hydrologic conditions. Smaller streams with channels above the aquifer tend to be intermittent (Beck and Arden 1983, Hayes et al. 1983). Regional base flow is supported by aquifer discharge (Hicks et al. 1987).

Row-crop agriculture and managed forestlands are the dominant land use within the region (~50% agriculture, ~30% forests) (Golladay and Battle 2001). In 1999, ~85% of agricultural lands in the lower FRB were irrigated, mostly by withdrawals from the Upper Floridan aquifer (Litts et al. 2001). Water use is estimated at 25 cm, ~20% of long-term average annual precipitation of 127 cm (Harrison 2001, Thomas et al. 2001).

Average daily discharge, based on 50 y of continuous streamflow records, has declined during the growing season since the development of irrigation in the 1970s (Stamey 1996). A modeling study predicted that groundwater withdrawals from the Upper Floridan aquifer during droughts could diminish aquifer–stream connections resulting in the drying of some reaches in the lower FRB (Albertson and Torak 2002). Water use from both groundwater and stream sources during extended droughts contributes to stream drying, although the extent has not been quantified.

Site selection

Mussel surveys were conducted at 21 sites on the tributary streams in the lower FRB from June to September 2001 (Fig. 1). These sites were a subset of those that had been previously surveyed in 1999 as part of an assessment of mussel populations in the lower FRB (Johnson 2001). Sites were selected for resurvey if they supported abundant and/or diverse mussel assemblages in 1999 (Johnson 2001). Where possible, sites were selected at regular intervals from headwaters downstream. Bridge crossings provided access for the surveys. A 100-m survey reach was measured and marked at each site. Reaches began 100 m upstream from bridge crossings.

An additional site was added to the survey in 2001 (01–001) (Fig. 1). This site supported an abundant and diverse mussel assemblage (10 species). The site was sampled during June and again in October 2001 to evaluate the repeatability of our sampling techniques.

Streamflow conditions during the drought

The drought in the lower FRB began in early 1999 and extended through the summer of 2002. The drought reached its maximum severity during the summer of 2000, based on Palmer Drought Severity indices (NCDC 2003, Fig. 2A). Palmer indices during the summer of 2000 ranged from −3 to −4, which are considered a severe to exceptional drought (USGS 2000, NCDC 2003).

Ichawaynochaway Creek, in the central portion of our study area (Fig. 1), has a USGS stream flow gauge (number 02353500) with a continuous record since 1940 (USGS 2003). Stream flow here was below the long-term mean from March 1999 through September 2002 (Fig. 2B). However, lowest flows were observed during June and August 2000 and were 10 to 20%

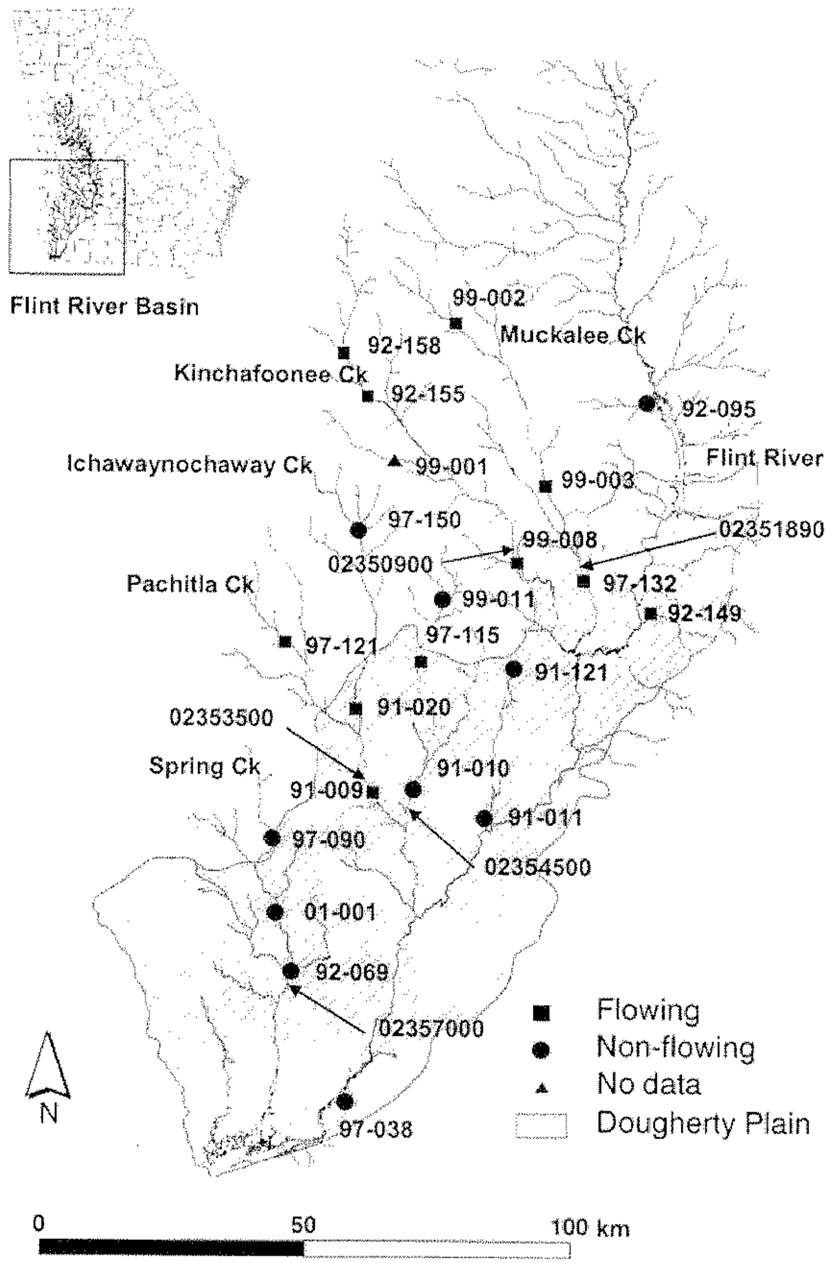

FIG. 1. Location of mussel survey sites (5-digit numbers) in southwestern Georgia. Sites designated as "non-flowing" had no observable surface flow for at least one month during summer 2000. Sites designated as "no data" were not observed during the 2000 drought. Locations of stream gauging stations (8-digit numbers) are indicated with arrows (USGS 2003). Site numbers: the first 2 digits are the year initially surveyed and the last 3 digits are the survey number for that particular year. Ck = creek.

of the long-term mean (Fig. 2B, Table 1). Similar declines in flow were observed at stream gauges throughout the region (Table 1). During June 2000, daily stream flow ranged from 0.7 to 17% of the long-term mean. During August 2000, stream flow ranged from 0 to 32% of the long-term mean (Table 1).

Most of the mussel survey sites were not gauged. Survey sites were visited weekly or bi-weekly, during the summer of 2000, and the

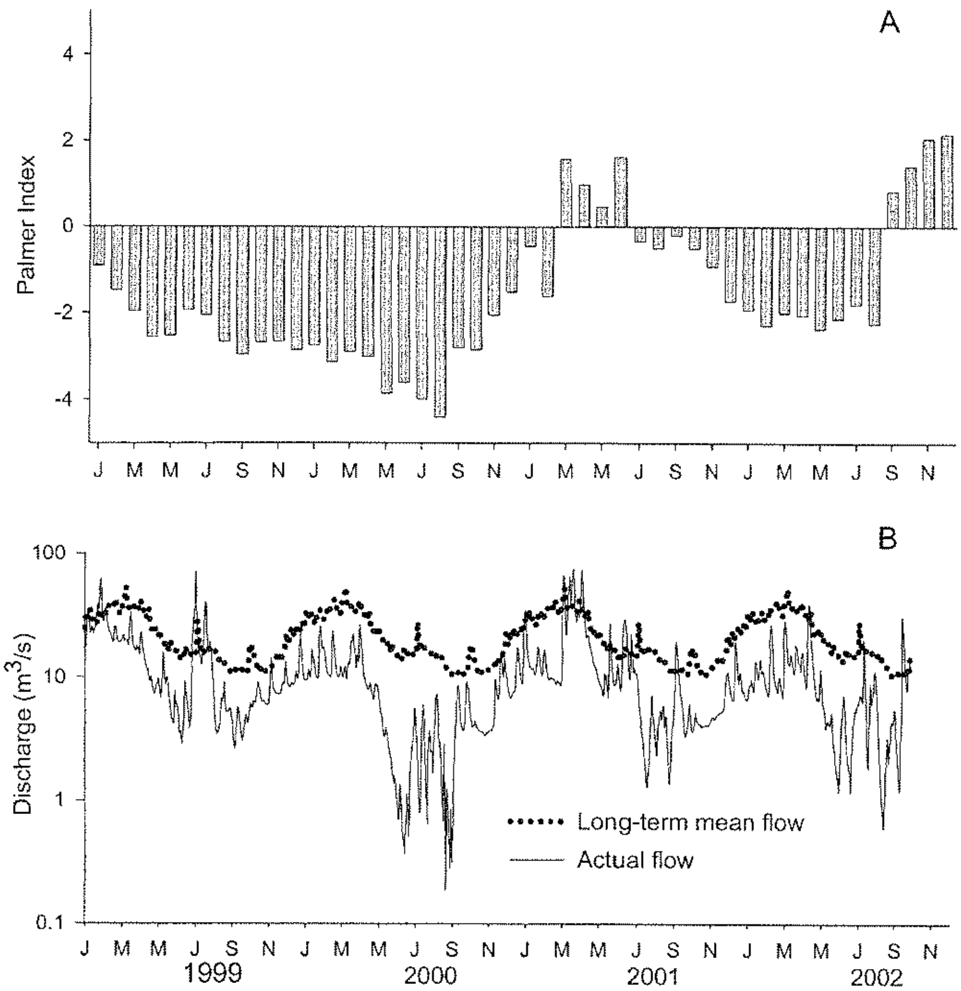

FIG. 2. Drought severity (NCDC 2003) (A) and streamflow (Ichawaynochaway Creek at Milford, US Geological Survey 02353500; USGS 2003) (B) in southwestern Georgia from 1999 through 2002.

TABLE 1. Mean monthly flows for 2000 and long-term mean monthly flows at stream gauging stations in the lower Flint River Basin (USGS 2003). Hydrologic classification was based on visual observations during the summer of 2000 at mussel survey reaches near the stream gauging stations.

		Mean monthly flow (m^3/s)		%	
		2000	Long-term	(2000/ long-term)	Hydrologic classification
Spring Creek	June	0.05	7.99	0.7	Non-flowing
	August	0.00	7.16	0.0	
Ichawaynochaway Creek	June	1.18	15.27	12.3	Flowing
	August	2.74	13.49	20.3	
Chickasawhatchee Creek	June	0.07	3.10	2.3	Flowing
	August	0.06	3.78	1.6	
Kinchafoonee Creek	June	1.33	7.82	17.0	Flowing
	August	1.87	5.93	31.5	
Muckalee Creek	June	0.94	5.89	16.0	Flowing
	August	1.39	5.16	26.9	

flow conditions at each study reach were documented by field observations of Jones Center Staff (i.e., Golladay and Battle 2001, Johnson et al. 2001, S. Davis, Jones Research Center, unpublished data). Sites were classified as flowing if they had observable moving water in the main channel during the worst drought conditions (Fig. 1). Sites classified as non-flowing either dried completely, or dried to small isolated pools with no surface flow between pools. Ten sites were classified as non-flowing and 7 of those sites occurred on the Dougherty Plain, including site 01–001 (Johnson 2001) (Fig. 1).

Wood debris measurements

Wood debris was measured during July and August 1999. At each survey site, a meter tape was extended midchannel for the length of the survey reach. Coarse wood debris (logs >10 cm in diameter) intersecting the tape was measured and counted. Debris frequency was expressed as logs per m stream length.

Mussel surveys

Measured survey reaches were searched at each site for mussels using standardized methods (e.g., Johnson 2001). In small streams, the entire bed surface within the selected survey reach was searched (i.e., surface sediments were sieved with fingers to a depth of 5 cm) or visually searched for live unionids. In large streams (4^{th} order or larger; >12 m wide), visual and tactile searches for live mussels were conducted along five 2-m wide transects oriented parallel to stream flow along the length of the stream reach (2 bank, 2 near bank, 1 midchannel). Root mats along stream margins were also searched. Surveys were conducted in the main channel(s) of the stream; backwater areas were not searched. Our objective was to search the same areas within each reach in 1999 and 2001. The drought persisted through 2001, but flow conditions at survey sites improved compared to the previous summer (e.g., Fig. 2A, B). The entire stream bottom of all survey sites was wetted.

Live mussels were identified and immediately returned to their original orientation within the benthic substrate. Mussels were not removed from stream water unless it was absolutely essential for identification. If >1000 individuals of any species were found before surveying to the end of a reach, the density of the species in the completed portion was calculated and the total density for the reach was estimated. Unionids were identified to species level, except *Elliptio complanata* and *Elliptio icterina*, which were grouped together as *E. complanata/icterina* because of the difficulty of distinguishing between the 2 species in the field. Taxonomic identification followed Turgeon et al. (1998) and Brim Box and Williams (2000). Shell material was collected and deposited at the Georgia Museum of Natural History, Athens, Georgia.

Data analysis

Mussel taxa found during the 1999 and 2001 surveys were placed into 3 categories based on their conservation status (Williams et al. 1993, Brim Box and Williams 2000, Georgia Department of Natural Resources 2003). The 1^{st} group consisted of common species whose populations are considered stable in the lower FRB and throughout their historical range. The 2^{nd} group was special concern species, which are listed as being imperiled in Georgia because of their rarity (Brim Box and Williams 2000, Georgia Department of Natural Resources 2003). The 3^{rd} group was endangered species, which have experienced significant declines throughout their historic range and are listed by the US Fish and Wildlife Service as at risk for extinction (Williams et al. 1993, Brim Box and Williams 2000).

The repeatability of our sampling procedure was assessed at site 01–001 (see above) by comparing mussel species richness, species abundance, and abundance by conservation status. Mussel abundance was compared with similarity indices using the Czekanowski Coefficient (Kent and Coker 1994).

The hydrologic classification (i.e., flowing or non-flowing during summer 2000) was used as the basis of statistical analysis of drought impacts on mussels. Changes in species richness, mussel species abundance, and abundance by conservation status were compared using a Wilcoxon Signed Rank Test (Sigma-Stat version 2.03, SPSS Science, Chicago, Illinois). The Signed Rank Test is a paired, nonparametric procedure that compares the change in the value of pairs of replicate measures (mussel abundances by species and conservation status) before and after a treatment (maintaining or not maintaining

TABLE 2. Comparison of 1999 and 2001 mussel surveys by species. Twenty-one sites were surveyed each year. Conservation status was based on Williams et al. (1993), Brim Box and Williams (2000), and Georgia Department of Natural Resources (2003).

Conservation status Species		Total found 1999 (sites found 1999)	Total found 2001 (sites found 2001)
Stable species			
Elliptio complanta/icterina		6208 (21)	6428 (20)
Elliptio crassidens		1937 (6)	1055 (7)
Toxolasma paulus		231 (13)	427 (12)
Uniomerus carolinianus		46 (10)	74 (10)
Villosa lienosa		1632 (20)	1720 (16)
Villosa vibex		390 (16)	766 (18)
	Sum	10,444	10,470
	%	94	93
Special concern species			
Elliptio purpurella		99 (10)	161 (8)
Lampsilis straminea claibornensis		20 (9)	8 (1)
Quincuncina infucata		360 (14)	543 (11)
Strophitus subvexus		10 (4)	9 (5)
Villosa villosa		31 (3)	1 (1)
	Sum	520	722
	%	5	6
Endangered species			
Lampsilis subangulata		131 (11)	56 (7)
Medionidus penicillatus		9 (2)	17 (1)
Pleurobema pyriforme		42 (5)	87 (6)
	Sum	182	160
	%	1	1

flow during the drought). This analysis was done on all of the species with a stable conservation status. To be included in the analysis, a species had to be present at a site on one of the survey dates. Sites where a particular species was not present on either date were not included in the analysis. Special concern and endangered species were not present at enough sites to be analyzed at the species level.

Mussel survey sites were also grouped based on whether or not they showed declines (>15%) in mussel abundance independent of their flow status. The frequency of wood debris at sites with declines >15% was compared to sites without declines using a *t*-test (Sigma-Stat version 2.03).

Results

A total of 11,146 mussels was observed in 1999 and a total of 11,352 was observed in 2001 (Table 2). Most mussels observed (93 to 94%) were species whose conservation status was stable. Special concern species represented 5 to 6% and endangered species represented 1% of mussels observed (Table 2). Three species, *Elliptio complanata/icterina*, *E. crassidens*, and *Villosa lienosa* were dominant in abundance and distribution at the study sites.

Six sites experienced >50% loss in total mussel abundance from 1999 to 2001 (Fig. 3). Five of these sites were located on the Dougherty Plain. Ten sites had increases or no changes in mussel numbers from 1999 to 2001 (Fig. 3). Five of the 6 sites that showed the greatest increases in abundance from 1999 to 2001 were located north of the Dougherty Plain (Fig. 3).

A total of 17 mussel taxa were found during the 2001 survey compared to 19 taxa during 1999. The 2 taxa not observed in 2001 were *Utterbackia imbecillis* and *U. peggyae*; however, they were found in low numbers at only one site during the 1999 survey. *Lampsilis teres* was reported from one site in 2001, but not observed in 1999.

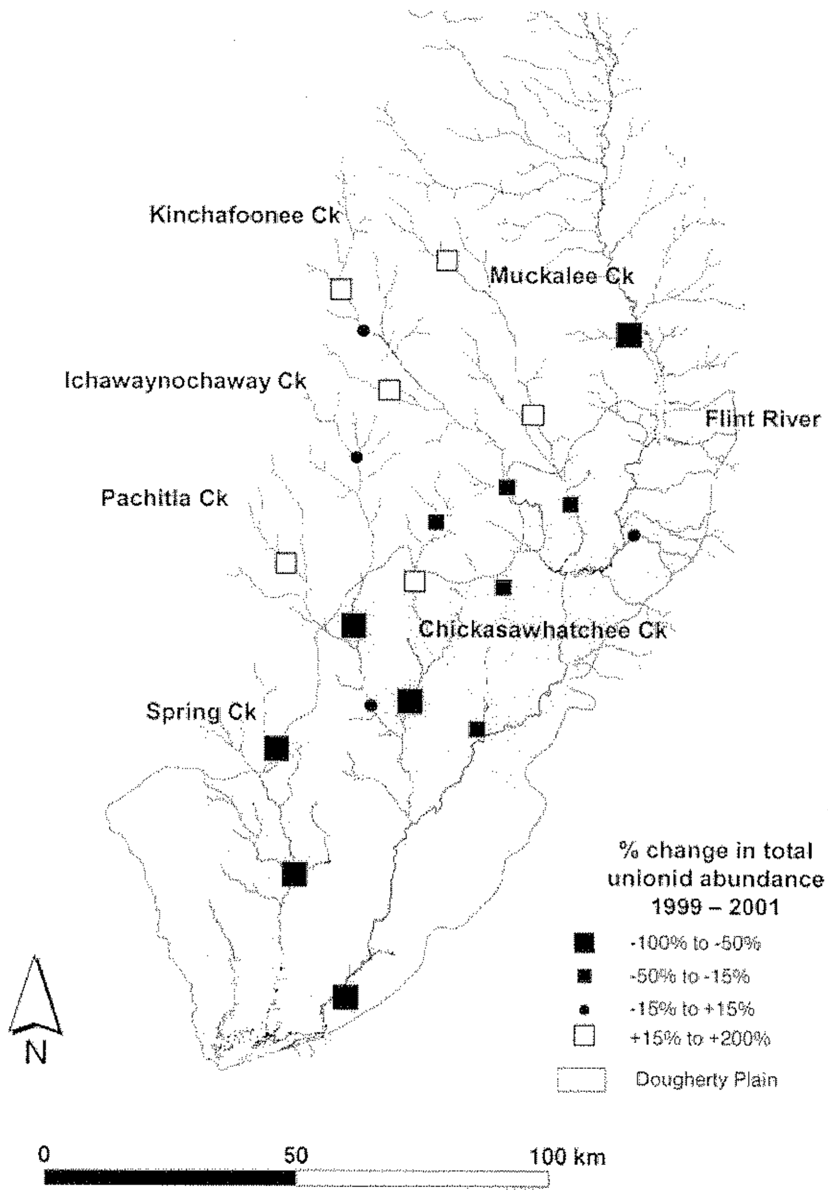

FIG. 3. Percent change in total unionid abundance in the lower Flint River Basin between 1999 and 2001. Ck = creek.

Utterbackia imbecillis, *U. peggyae*, and *L. teres* typically occur in larger rivers and impoundments on mainstem rivers that were not surveyed in this study (Brim Box and Williams 2000).

At site 01–001 in 2001, 372 mussels were found in June (9 species) and 425 mussels were found in September (10 species) (Table 3). Czekanowski similarity indices between the 2 sampling dates were 79% for individual mussel species abundance and 92% when grouped by conservation status. Three species, *E. complanata/icterina*, *Pleurobema pyriforme*, and *Toxolasma paulus* showed the greatest variation across sampling dates. The difference in abundance of individuals observed across sampling dates was 10 or less for the remaining 6 species.

The median number of stable species at flowing sites significantly increased from 226 to 314 per site from 1999 to 2001 ($p = 0.02$; Table 4). The increase was caused by significantly higher numbers of *E. complanata/icterina* ($p = 0.03$) and *Villosa vibex* ($p = 0.04$) in the 2001 survey. There were no other significant differences in numbers of stable species across survey dates. Numbers of special concern species, endangered species, and taxa did not significantly change from 1999 to 2001 at sites classified as flowing (Table 4).

The median number of stable species at non-flowing sites declined significantly from 181 to 71 per site from 1999 to 2001 (p = 0.01; Table 4). Declines were caused by significantly lower numbers of *E. complanata/icterina* (p = 0.02) and *V. lienosa* (p = 0.004) observed in 2001. Taxa richness also was significantly lower at non-flowing sites in 2001 compared to 1999 (p = 0.02). There was no significant difference in special concern species at non-flowing sites. However, endangered species showed a tendency to decline (1999: 27 versus 2001: 2), although the difference was not significant (p = 0.1; Table 4).

Wood debris frequency was significantly greater (p = 0.002) (mean: 0.33 logs/m, SD: 0.18, n = 10) at sites where mussel populations did not decline during the drought compared to sites where declines were observed (mean: 0.11 logs/m, SD: 0.10, n = 11).

TABLE 3. Comparison of mussel surveys conducted in June and September 2001 at site 01-001 in the Spring Creek drainage of southwestern Georgia.

Conservation status / Species		Total found: June	Total found: September
Stable species			
Elliptio complanta/icterina		102	59
Elliptio crassidens		0	2
Toxolasma paulus		16	59
Uniomerus carolinianus		1	4
Villosa lienosa		49	50
Villosa vibex		33	23
	Sum	201	197
Special concern species			
Elliptio purpurella		1	4
Lampsilis straminea claibornensis		18	14
	Sum	19	18
Endangered species			
Lampsilis subangulata		23	23
Pleurobema pyriforme		129	187
	Sum	152	210

Discussion

Mussel responses to drought

Deforestation, intensive upland agricultural development, river impoundments, and declines in native fish species have adversely affected mussel diversity and abundance in the lower FRB (Brim Box and Williams 2000). Infrequent natural disturbances such as droughts may further affect mussels by causing physiological stress or death to individuals or populations already stressed by habitat alteration.

Freshwater mussels are limited in their ability to migrate. They must be able to tolerate the physical and chemical conditions of their immediate environment to survive. Droughts are usually prolonged, exposing mussels to stressful conditions for extended periods. Early in a drought, decreases in water depth and flow velocity reduce food and oxygen delivery. As droughts persist, mussels face hypoxia, increasing water temperature and, ultimately, anoxia or emersion (being stranded out of water and exposed to air). Mussels have adaptations to a wide range of environmental conditions, but many species are considered sensitive to disturbance and are unable to withstand low dissolved oxygen (DO) concentrations and high water temperature (Fuller 1974).

Mussels also may suffer lethal and nonlethal impacts from drought-related habitat change. Increases in water temperature may shorten the period of glochidial encystment, slow righting, burrowing and movement responses, and increase oxygen consumption (Young 1911, Bartsch et al. 2000). Low DO concentration impairs respiration, slows growth, reduces glycogen stores, and may inhibit reproduction (Fuller 1974). Reduced flow velocity during drought may be insufficient to suspend glochidia and superconglutinates (larval mussel masses), resulting in reproductive failure (M. Freeman, University of Georgia, personal communication).

Several mechanisms for enduring drought-related environmental change have evolved among the Unionidae. Some freshwater mussels have the capacity to lower metabolic activity in response to temporary temperature changes and DO stress (e.g., *E. complanata*, *U. imbecillis*, *Pyganodon grandis*) (Bayne 1967, Burky 1983, Sheldon and Walker 1989, McMahon 1991). At least one freshwater species, *Anodonta implicata*,

TABLE 4. Median numbers and interquartile ranges of mussels observed per site for 11 flowing and 10 non-flowing sites in 1999 and 2001. Numbers of individuals were compared using a Wilcoxon Signed Rank Test.

	Median numbers		
	1999 (interquartile range)	2001 (interquartile range)	*p*-value
Flowing sites			
Elliptio complanata/icterina	106 (28–690)	176 (29–834)	0.03
Elliptio crassidens	1 (0–287)	1 (1–268)	0.8
Villosa lienosa	21 (11–110)	47 (9–95)	0.5
Toxolasma paulus	10 (4–25)	11 (8–44)	0.2
Uniomerus carolinianus	6 (1–8)	5 (4–10)	0.2
Villosa vibex	6 (3–29)	17 (4–61)	0.04
Stable spp. combined	226 (66–1009)	314 (60–1351)	0.02
Special concern spp. combined	20 (8–53)	22 (10–40)	0.6
Endangered spp. combined	3 (3–6)	6 (2–13)	0.2
Taxa richness	8 (7–10)	8 (6–9)	0.3
Non-flowing sites			
Elliptio complanata/icterina	108 (19–512)	51 (5–449)	0.02
Elliptio crassidens	40 (11–643)	10 (3–16)	0.2
Villosa lienosa	18 (12–62)	9 (0–39)	0.004
Toxolasma paulus	2 (1–19)	2 (0–4)	0.4
Uniomerus carolinianus	2 (0–2)	2 (0–2)	0.8
Villosa vibex	14 (4–34)	8 (2–66)	0.4
Stable spp. combined	181 (67–832)	71 (15–603)	0.01
Special concern spp. combined	3 (2–18)	1 (1–6)	0.7
Endangered spp. combined	27 (3–50)	2 (0–14)	0.1
Taxa richness	6 (6–8)	5 (4–6)	0.02

can produce metabolic oxygen in sufficient quantities to survive anoxic surroundings (Eddy and Cunningham 1934). Upon emersion, other Unionidae may respire through "mantle exposure behavior", a gaping behavior that permits the exchange of aerial gases through a mucus-sealed mantle margin (McMahon 1991). Other mussel species are able to switch from aerobic to anaerobic respiration during times of anoxia (Holland 1991). Another unionid adaptation is the ability to rapidly migrate deep into sediments to avoid emersion (White 1979).

Johnson (2001) documented several primary causes of mussel mortality in the lower FRB during drought. Dissolved oxygen levels declined in streams as flow decreased. Mussel species vary in their tolerances to low DO (see below), but accelerated mussel mortality was observed as DO levels dropped below 5 mg/L (Johnson 2001). Low flows were also associated with increased mussel predation by raccoons at some sites. Thin-shelled species like *V. lienosa* and *V. vibex* were particularly susceptible (Johnson 2001). High densities of the exotic *Corbicula fluminea* were also associated with native mussel mortality. *Corbicula fluminea* is relatively intolerant of hypoxia (McMahon 1979) and died before native mussel species. However, decay of *C. fluminea* accelerated stream stagnation and resulted in native mussel mortality (Johnson 2001).

Freshwater mussel species in the lower FRB vary in their tolerances to drought stresses. Several of the special concern and endangered species appeared to be drought intolerant. Johnson (2001) observed accelerated mortality of *Lampsilis straminea clairbornensis*, *Lampsilis subangulata*, *P. pyriforme*, and *Medionidus penicillatus* at DO levels below 5 mg/L. Several of the stable species, *E. complanata/icterina*, *V. vibex*, and *V. lienosa* were relatively uneffected by low DO concentrations (Johnson 2001). *Elliptio complanata/icterina*, *V. vibex*, and *V. lienosa* were also observed to withstand extended periods of emersion (Johnson 2001). *Elliptio crassidens* was sensitive to low DO concentrations but tended to be limited to large streams that maintained flow (Johnson 2001).

In our study, changes in total mussel abundance between 1999 and 2001 varied greatly, ranging from a 93% decrease to a 180% increase (Fig. 3). Greatest declines in mussel abundance were associated with stream drying that occurred in the mid-reaches of the major tributaries of the lower Flint River. However, drying did not result in decreases in mussel abundance at all non-flowing sites. For example, mussel populations remained stable at site 97–150 even though flow ceased (Figs 1, 3). This site had extensive wood debris (0.33 logs/m). Johnson et al. (2001) observed that, as streams dried, mussels tended to congregate in small shaded depressions on the downstream side of wood debris in the streambed. Individuals that moved into depressions had greater survivorship during stream drying than those that remained in adjacent habitats (Johnson et al. 2001). The role of wood debris as a refuge for mussels during droughts has not been widely reported.

A substantial decline in mussel abundance was also observed at 2 of the flowing sites (91–020, 97–132; Figs 1, 3). Channel dredging was observed at site 91–020. Site 97–132 had poor midchannel mussel habitat (coarse sand) and low wood debris density (0.08 logs/m). At this site, most mussels were associated with roots and stumps along the streambank. Flow persisted at site 97–132, but channel shrinkage may have caused a decrease in mussel habitat.

Increases in mussel abundance observed at several flowing sites were not a result of reproduction, as few small individuals were observed during 2001 resurveys. The apparent increases are attributed to greater sampling efficiency because conditions for observing mussels were better at these sites (i.e., lower flows, clearer water) in 2001 compared to when they were sampled in 1999. All of the sites showing declining mussel populations were surveyed under comparable or more favorable conditions for observing mussels in 2001 than in 1999.

The results of our study generally concur with the observations of Johnson (2001). We observed substantial declines in mussel abundance in non-flowing streams, but substantial numbers of *E. complanata/icterina*, *V. lienosa*, and *V. villosa* survived at some of the sites. Several of the special concern species including, *L. s. claibornensis*, *V. villosa*, and *L. subangulata* showed declining trends or disappeared from a number of non-flowing sites suggesting intolerance to drought stress. The drought tolerance of other mussel species in the lower FRB remains undocumented.

Drought frequency in the southeastern US

Persistent droughts are a regular occurrence in the lower FRB and southeastern Coastal Plain. Droughts are associated with periodic El Nino–Southern Oscillation, cyclical variations in the tropical Pacific Sea surface temperatures (Hoerling and Kumar 2003). Droughts occur during extended cold phases (termed "La Nina"), which promote the formation of persistent high-pressure systems preventing the influx of moisture from the Gulf of Mexico (Golden and Hess 1991, Hoerling and Kumar 2003). Persistent droughts have occurred in the region in the 1930s, 1950s, 1980s, and late 1990s (Golden and Hess 1991).

The late 1990s drought (1998–2002) was not limited to the southeast but extended across the mid-latitudes of the Northern Hemisphere (Hoerling and Kumar 2003). The drought was associated with La Nina conditions in the Tropical Pacific Ocean and anomalous warming in the western Pacific and Indian Oceans. Global climate models associated the anomalous warming of the western Pacific and Indian Oceans to increased greenhouse gases in the atmosphere (Hoerling and Kumar 2003). There is uncertainty on whether conditions that led to the late 1990s drought will become more frequent as global climate change occurs. However, the potential exists for more frequent and extended droughts in the lower FRB under some global change scenarios (Hoerling and Kumar 2003).

Multiyear droughts have a major impact on hydrology of the lower FRB because aquifer recharge is reduced. Low recharge rates cause a gradual decrease in groundwater to support summer base flow in streams. Drought effects are compounded by human water use, which increases in the absence of normal rainfall. Because extensive human appropriation of water is a recent development, the severity of drought stress on streams and rivers in the lower FRB may be intensifying.

In conclusion, the greatest declines in mussel abundance in our study occurred in the mid-reaches of the major tributaries of the lower Flint River. Many of these areas dried completely during the drought conditions of the summer of 2000. The major tributaries of the lower FRB depend on the Upper Floridan aquifer, which is heavily used for irrigation, to maintain base flow. Declines in mussel populations appear to be associated with unusual climatic conditions and increasing demand on the streams in the area and the regional aquifer system for irrigation water supply. Thus, infrequent disturbances, such as the 2000 drought, stress the remaining populations and accelerate the loss of freshwater mussel diversity from the lower FRB.

The contribution of wood debris to the structure and function of Coastal Plain streams has been widely noted (e.g., Wallace and Benke 1984), but the potential for wood debris to act as a refuge for freshwater mussels has not been recognized previously. Historically, wood debris removal from streams was a common practice that provided wood products, facilitated navigation and recreation, and provided flood control (Wallace and Benke 1984). The practice still occurs in the southeastern Coastal Plain (SWG, personal observation). However, until the significance of wood for freshwater mussels has been further studied, wood removal should be avoided in areas where freshwater mussel conservation is a priority.

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Literature Cited

ALBERTSON, P. N., AND L. J. TORAK. 2002. Simulated effects of ground-water pumpage on stream-aquifer flow in the vicinity of federally protected species of freshwater mussels in the lower Apalachicola-Chattahoochee-Flint River Basin (Subarea 4), southeastern Alabama, northwestern Florida, and southwestern Georgia. U.S. Geological Survey Water-Resources Investigations Report 02-4016. US Geological Survey, Atlanta, Georgia.

BARTSCH, M. R., D. L. WALLER, W. G. COPE, AND S. GUTREUTER. 2000. Emersion and thermal tolerances of three species of unionid mussels: survival and behavioral effects. Journal of Shellfish Research 19:233–240.

BAYNE, B. L. 1967. Respiratory response of *Mytilus perna* to reduced environmental oxygen. Physiological Zoology 40:307–313.

BECK, B. F., AND D. D. ARDEN. 1983. Hydrogeology and geomorphology of the Dougherty Plain. Georgia Southwestern College, Americus, Georgia.

BRIM BOX, J., AND J. D. WILLIAMS. 2000. Unionid mollusks of the Apalachicola Basin in Alabama, Florida, and Georgia. Alabama Museum of Natural History Bulletin 21. Alabama Museum of Natural History, Tuscaloosa, Alabama.

BURKY, A. J. 1983. Physiological ecology of freshwater bivalves. Pages 281–327 *in* W. D. Russel-Hunter (editor). The Mollusca. Vol. 6: Ecology. Academic Press, New York.

CLENCH, W. J., AND R. D. TURNER. 1956. Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwanee River. Bulletin of the Florida State Museum 1:97–239.

EDDY, N. W., AND R. B. CUNNINGHAM. 1934. Oxygen consumption of the fresh-water mussel, *Anodonta implicata*. Proceedings of the Pennsylvania Academy of Sciences 8:140–143.

FULLER, S. L. H. 1974. Clams and mussels (Mollusca: Bivalvia). Pages 215–272 *in* C. W. Hart and S. L. H. Fuller (editors). Pollution ecology of freshwater invertebrates. Academic Press, New York.

GEORGIA DEPARTMENT OF NATURAL RESOURCES. 2003. Accessed September 2003. http://georgiawildlife.dnr.state.ga.us/content/specialconcernanimals.asp

GOLDEN, H. G., AND G. W. HESS. 1991. Georgia: floods and droughts. Pages 239–243 *in* National water summary 1988–1999. U.S. Geological Survey Water-Supply Paper 2375. US Geological Survey, Doraville, Georgia.

GOLLADAY, S. W., AND J. BATTLE. 2001. Does the Chickasawhatchee Swamp influence water quality? Pages 337–340 *in* K. J. Hatcher (editor). Proceedings of the 2001 Georgia Water Resources Conference. Institute of Ecology, University of Georgia, Athens, Georgia.

HARRISON, K. M. 2001. Agricultural irrigation trends in Georgia. Pages 114–117 *in* K. J. Hatcher (editor). Proceedings of the 2001 Georgia Water Resources Conference. Institute of Ecology, University of Georgia, Athens, Georgia.

HAYES, L. R., M. L. MASLIA, AND W. C. MEEKS. 1983. Hydrology and model evaluation of the principal artesian aquifer, Dougherty Plain, southwest Georgia. Georgia Geological Survey Information Circular 97. Georgia Geological Survey, Atlanta, Georgia.

HICKS, D. W., H. E. GILL, AND S. A. LONGSWORTH. 1987. Hydrogeology, chemical quality, and availability of ground water in the Upper Floridan aquifer, Albany, Georgia. U.S. Geological Survey Water-Resources Investigations Report 87-4145. US Geological Survey, Atlanta, Georgia.

HOERLING, M., AND A. KUMAR. 2003. The perfect ocean for drought. Science 299:691–694.

HOLLAND, D. F. 1991. Prolonged emersion tolerance in freshwater mussels (Bivalvia: Unionidae): interspecific comparison of behavioral strategies and water loss rates. MSc Thesis, University of Texas at Arlington, Arlington, Texas.

JOHNSON, P. M. 2001. Habitat associations and drought responses of freshwater mussels in the lower Flint River Basin. MSc Thesis, University of Georgia, Athens, Georgia.

JOHNSON, P. M., A. E. LINER, S. W. GOLLADAY, AND W. K. MICHENER. 2001. Effects of drought on freshwater mussels and instream habitat in Coastal Plain tributaries of the Flint River, southwest Georgia (July–October 2000). Final Report submitted to The Nature Conservancy Apalachicola River and Bay Project. Nature Conservancy, Apalachicola, Florida. (Available from: http://www.jonesctr.org/research/aquatics_research/creeks_mussels_2.html)

KENT, M., AND P. COKER. 1994. Vegetation description and analysis. John Wiley and Sons, Chichester, UK.

LITTS, T., H. RUSSELL, A. THOMAS, AND R. WELCH. 2001. Mapping irrigated lands in the ACF river basin. Pages 79–83 *in* K. J. Hatcher (editor). Proceedings of the 2001 Georgia Water Resources Conference. Institute of Ecology, University of Georgia, Athens, Georgia.

MCMAHON, R. F. 1991. Mollusca: Bivalvia. Pages 315–399 *in* J. H. Thorpe and A. P. Covich (editors). Ecology and classification of North American freshwater invertebrates. Academic Press, New York.

NCDC (NATIONAL CLIMATE DATA CENTER). 2003. CLIMVIS (Climate Visualization) home page. Accessed September 2003. http://www.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmgr.html

SHELDON, R., AND K. F. WALKER. 1989. Effects of hypoxia on oxygen consumption by two species of freshwater mussel (Unionacea: Hyriidae) from the River Murray. Australian Journal of Marine and Freshwater Research 40:491–499.

STAMEY, T. C. 1996. Streamflow characteristics at selected sites in southwestern Georgia, southeastern Alabama, and northwestern Florida, Near Lake Seminole. U.S. Geological Survey Open-File Report 95–455. US Geological Survey, Atlanta, Georgia.

THOMAS, D. L., K. A. HARRISON, J. E. HOOK, G. HOOGENBOOM, R. W. MCCLENDON, L. WHEELER, W. I. SEGARS, J. MALLARD, G. MURPHY, M. LINDSAY, D. D. COKER, T. WHITLEY, J. HOUSER, S. CROMER, AND C. MYERS-ROCHE. 2001. Status of ag. water pumping: a program to determine agricultural water use in Georgia. Pages 101–104 *in* K. J. Hatcher (editor). Proceedings of the 2001 Georgia Water Resources Conference. Institute of Ecology, University of Georgia, Athens, Georgia.

TURGEON, D. D., J. F. QUINN., A. E. BOGEN, E. V. COAN, F. G. HOCHBERG, W. G. LYONS, P. M. MIKKELSEN, R. J. NEVES, C. F. E. ROPER, G. ROSENBERG, B.

ROTH, A. SCHELTEMA, F. G. THOMPSON, M. VECCHIONE, AND J. D. WILLIAMS. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada. 2nd edition. American Fisheries Society Special Publication 26. American Fisheries Society, Bethesda, Maryland.

USGS (UNITED STATES GEOLOGICAL SURVEY). 2000. Georgia drought watch website. Summary of hydrologic conditions: September 2000 and earlier. Accessed October 2000. http://ga.water.usgs.gov/news/drought99

USGS (UNITED STATES GEOLOGICAL SURVEY). 2003. Real-time data for Georgia: steamflow homepage. Accessed September 2003. http://waterdata.usgs.gov/ga/nwis/current/?type=flow&group_key=basin_cd

WALLACE, J. B., AND A. C. BENKE. 1984. Quantification of wood habitat in subtropical Coastal Plain streams. Canadian Journal of Fisheries and Aquatic Sciences 41:1643–1652.

WHITE, D. S. 1979. The effect of lake level fluctuations on *Corbicula* and other pelecypods in Lake Texoma, Texas and Oklahoma. Pages 82–88 *in* J. C. Britton (editor). Proceedings, First International *Corbicula* Symposium. Texas Christian University Research Foundation, Fort Worth, Texas.

WILLIAMS, J. D., M. L. WARREN, K. S. CUMMINS, J. L. HARRIS, AND R. J. NEVES. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18(9):6–22.

YOUNG, D. 1911. The implantation of the glochidium on the fish. University of Missouri Bulletin of Scientific Series 2:1–20.

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