

**Abstract**—Our study goal was to characterize the demographics of the population of Hickory Shad (*Alosa mediocris*) in the Albemarle Sound–Roanoke River watershed during a period of population increase and to assess its susceptibility to harvest. Adults were collected from gillnet surveys and a river recreational fishery from February to May 1996. The male-to-female ratio was similar between the Albemarle Sound (0.73:1) and the spawning grounds in Roanoke River (0.76:1). Ages were 2–7 years, but most sampled fish were age 3 or 4. The von Bertalanffy growth equation was  $L_t = 460 (1 - e^{-0.24(t + 1.63)})$ , where  $L_t$  was predicted length at time  $t$  for sexes combined. Total mortality ( $Z$ ) was 1.43 for males age 3–5, 1.76 for females age 4–6, and 1.40 for sexes combined. Sexual maturity in both sexes was essentially complete by age 4. Repeat spawning was common: 46.8% of males were virgin, 45.5% had spawned once, and 7.7% had spawned 2 or 3 times. For females, 24.9% were virgin, 45.5% had spawned once, and 29.6% showed evidence of spawning 2, 3, or 4 times. Mesentery fat in both sexes decreased from the prespawning aggregation (staging) area in the sound to the river spawning grounds, indicating that both sexes feed extensively in ocean waters before the inland portion of the spawning migration. The short lifespan of Hickory Shad, combined with an early age to maturity and an anadromous migration pattern, indicates that mature individuals are very susceptible to recreational and commercial harvest and are removed by exploitation or natural mortality within 1 or 2 seasons.

Manuscript submitted 31 January 2014.  
Manuscript accepted 27 May 2014.  
Fish. Bull. 112:221–236 (2014).  
doi:10.7755/FB.112.2-3.8

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## Population demographics of Hickory Shad (*Alosa mediocris*) during a period of population growth

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Hickory Shad (*Alosa mediocris*) is 1 of 4 anadromous *Alosa* species native to the East Coast of North America. The other species are American Shad (*A. sapidissima*) and the river herrings Blueback Herring (*A. aestivalis*) and Alewife (*A. pseudoharengus*). Often, Hickory Shad is confused with American Shad, and they commonly appear together in local fish markets. Hickory Shad ranges from Cape Cod, Massachusetts, to the St. Johns River, Florida (Robins et al., 1986) and there is no evidence of spawning populations north of Maryland (Richkus and DiNardo<sup>1</sup>). It is assumed that this species returns to natal streams to spawn as does American Shad (Melvin et al., 1986), but homing has not been documented. Hickory Shad typically are 30–45 cm in fork length (FL) and 0.5–1.0 kg in weight—size ranges that are intermediate between the larger American Shad and smaller river herrings (Robins et al., 1986).

The center of abundance for Hickory Shad is thought to be in North Carolina because historically the North Carolina commercial fishery landed the greatest number of Hickory Shad among the fisheries along the U.S. eastern seaboard (Atlantic States Marine Fisheries Commis-

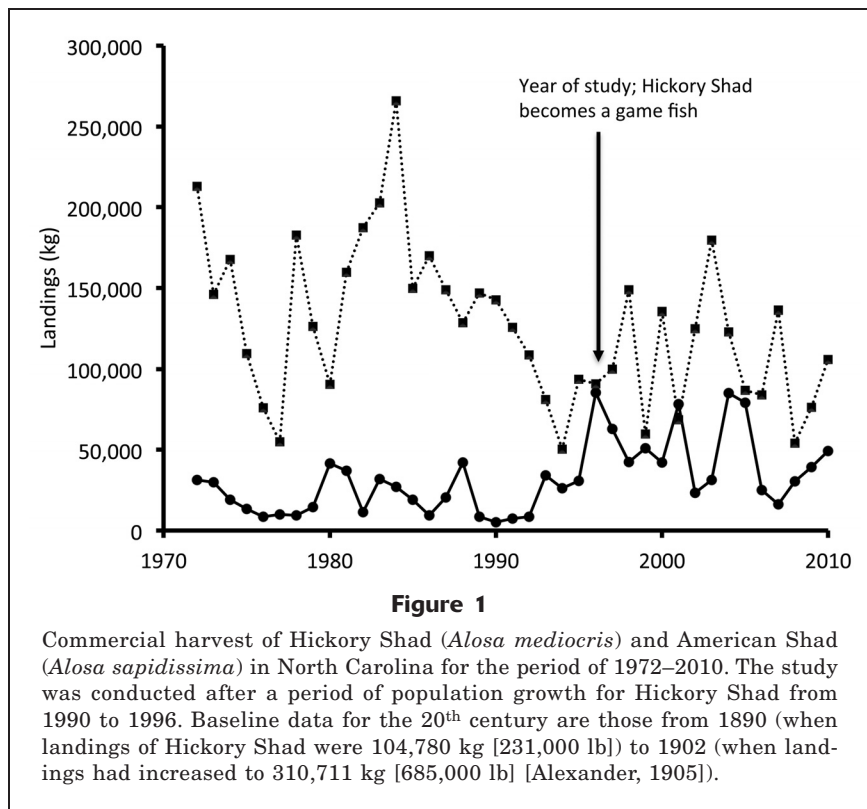
sion [ASMFC]<sup>2</sup>). In 1902, the Hickory Shad harvest from North Carolina through Florida was 351,970 kg (775,962 lb) and worth \$37,709 (approximately \$900,000 in 2011 dollars); North Carolina fisheries landed 88.3% of the total and represented 90.0% of the dockside value (Alexander, 1905). By 2001, the species was an incidental catch in various North Carolina gillnet fisheries in Albemarle and Pamlico sounds and in the coastal Atlantic Ocean (North Carolina Division of Marine Fisheries [NCDMF]<sup>3</sup>). Hickory Shad also were landed from pound nets, haul seines, and the nearshore ocean winter trawl fishery (Street et al.<sup>4</sup>).

<sup>2</sup> ASMFC (Atlantic States Marine Fisheries Commission). 1999. Amendment 1 to the interstate fishery management plan for shad and river herring. Fishery Management Report No. 35, 76 p. ASMFC, Washington, D.C. [Available from <http://www.asmf.org/uploads/file/shadam1.pdf>.]

<sup>3</sup> NCDMF (North Carolina Division of Marine Fisheries). 2001. Assessment of North Carolina commercial finfisheries, 1997–2000. Final performance report for Award Number NA 76 FI 0286, segments 1–3, 365 p. [Available from Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, 3441 Arendell St., Morehead City, NC 28557.]

<sup>4</sup> Street, M. W., P. P. Pate, B. F. Holland Jr., and A. B. Powell. 1975. Anadromous fisheries research program, northern coastal region, North Carolina. Final report for Project AFCS-8, 210 p. Division of Marine Fisheries, North Carolina Department of Natural and Economic Resources, Morehead City, NC.

<sup>1</sup> Richkus, W. A., and G. DiNardo. 1984. Current status and biological characteristics of the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring, 248 p. Atlantic States Marine Fisheries Commission, Washington, D.C.



During the 1990s, Hickory Shad populations increased, whereas populations of the other 3 *Alosa* species of the eastern seaboard decreased (Rulifson, 1994; Waldman and Limburg, 2003; Watkinson, 2004). This trend was evident in the commercial landings data for North Carolina (Fig. 1). Federal and state landings data for shads are sometimes difficult to interpret because often Hickory Shad are not separated from landings of American Shad. However, personnel of state fisheries agencies and recreational fishermen have noted these increases through much improved springtime opportunities (e.g., catches and abundance) in the recreational fishery throughout the range of the Hickory Shad. In North Carolina and other mid-Atlantic states, sportfishing for Hickory Shad is now common during February, March, and April, when adults ascend rivers to spawn before the other 3 *Alosa* species; this shad is also popular as a secondary target in the spring sport fisheries for White Perch (*Morone americana*) and Striped Bass (*M. saxatilis*). The Roanoke River watershed just downstream of the last dam at Roanoke Rapids, North Carolina, and the tributary Cashie River near the town of Windsor are popular areas for Hickory Shad sportfishing (Fig. 2). Angler harvest in the Roanoke River watershed increased from a 1968 estimate of 143 Hickory Shad caught by rod and reel and 2377 fish caught by special devices, such as dip nets and gill nets (Baker<sup>5</sup>),

<sup>5</sup> Baker, W. D. 1968. A reconnaissance of anadromous fish

to a 1996 estimate of 58,621 fish caught by hook and line that did not include the significant harvest by bank anglers (Kornegay<sup>6</sup>).

In 1996, concerns about overharvesting caused the North Carolina Wildlife Resources Commission (NCWRC) to classify Hickory Shad as a game fish in inland waters (Fig. 1). Since then, the bag limit has been 10 shads in aggregate per day (but only 1 American Shad) in inland, estuarine, and coastal waters (ASMFC<sup>2</sup>). Subsequently, the recreational fishery for Hickory Shad and Striped Bass in the Roanoke River has turned into a multimillion-dollar activity (McCargo et al.<sup>7</sup>). In 2006, anglers expended 14,065 hours (standard error of the mean [SE] 11,589), primarily in March and April. An estimated 81% of the shad were released; the remainder was harvested, but only 1.4% of that remainder were American Shad—indicating the importance of Hickory Shad to the sport fishery. Similar trends have been observed in the nearby Neuse River watershed, which has supported

a long-standing shad sport fishery (Marshall, 1977; Hawkins<sup>8</sup>; Manooch, 1984).

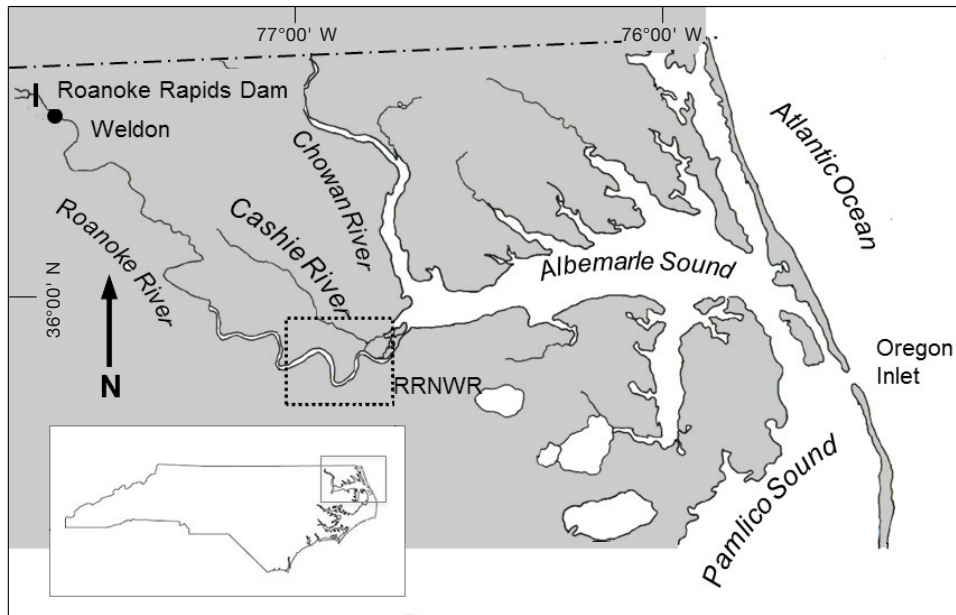
A comprehensive review of Hickory Shad populations in South Atlantic coastal states was conducted by Rulifson et al. (1982), who documented that many of the life history aspects of this species were unknown. Since then, life history aspects of the Hickory Shad have been studied in Virginia rivers by Watkinson (2004), the Roanoke River by Batsavage (1997) and Harris and Hightower (2010, 2011), the Tar-Pamlico River by Smith (2006), Murauskas (2006), and Murauskas and Rulifson (2009, 2011), and the Neuse River by Burdick and Hightower (2006), al-

runs into the inland fishing waters of North Carolina. Final report for Project AFS-3, 38 p. [Available from Division of Inland Fisheries, North Carolina Wildlife Resources Commission, 1751 Varsity Dr., Raleigh, NC 27606.]

<sup>6</sup> Kornegay, J. W. 1996. Unpubl. data. North Carolina Wildlife Resources Commission, 1751 Varsity Dr., Raleigh, NC 27606.

<sup>7</sup> McCargo, J. W., K. J. Dockendorf, and C. D. Thomas. 2007. Roanoke River recreational angling survey, 2005–2006. Final report, Coastal Fisheries Investigations, Federal Aid in Fish Restoration Project F-22, 67 p. [Available from Division of Inland Fisheries, North Carolina Wildlife Resource Commission, 1751 Varsity Dr., Raleigh, NC 27606.]

<sup>8</sup> Hawkins, J. H. 1980. Investigations of anadromous fishes of the Neuse River, North Carolina. Special Scientific Report. No. 34, 111 p. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC.



**Figure 2**

Map of the lower Roanoke River watershed and Albemarle Sound in North Carolina, showing the general locations where adult Hickory Shad (*Alosa mediocris*) were collected during February–May 1996 from 2 independent gillnet surveys in the western end of Albemarle Sound, in the Roanoke River National Wildlife Refuge (RRNWR; indicated with dotted rectangle), and in the recreational fishery on the spawning grounds of Hickory Shad near the city of Weldon, North Carolina.

though none except Batsavage (1997) were focused on age and growth. At the southern end of its range in Florida, the St. Johns River population was studied early by Walberg (1960) and Williams and Bruger<sup>9</sup>. In North Carolina, no directed sampling by state agencies has been conducted since 1993, but the NCWRC has collected Hickory Shad data for the 4 major North Carolina coastal rivers (Roanoke, Tar-Pamlico, Neuse, and Cape Fear) between 2000 and 2010 with annual monitoring (Dockendorf<sup>10</sup>).

Understanding key aspects of the life history, as well as the stock status of individual populations, is critical for species management. The ASMFC has long identified life history aspects and the stock status of Hickory Shad as priorities for future research (Richkus and DiNardo<sup>1</sup>; ASMFC<sup>11,12,13</sup>).

The goal of our study was to characterize the demographics of Hickory Shad during a known period of stock rebuilding with the Albemarle Sound–Roanoke River watershed as the focus population because of the important commercial and recreational fisheries there that target Hickory Shad. We describe the age, size, sex ratio, fecundity, age to maturity, growth, and mortality of adult Hickory Shad in the spring prespawning population in Albemarle Sound and during the spawning run near the spawning region in the Roanoke River near Weldon, North Carolina. Results of this study provide important life history information for future management plan development.

<sup>9</sup> Williams, R. O., and G. E. Bruger. 1972. Investigations on American shad in the St. Johns River. Technical Series No. 66, 49 p. Florida Department of Natural Resources, St. Petersburg, FL. [Available from [http://research.myfwc.com/publications/publication\\_info.asp?id=29934](http://research.myfwc.com/publications/publication_info.asp?id=29934).]

<sup>10</sup>Dockendorf, K. 2013. Personal commun. North Carolina Wildlife Resources Commission, Raleigh, NC 27606.

<sup>11</sup>ASMFC (Atlantic States Marine Fisheries Commission). 1985. Fishery management plan for the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. Phase II in interstate management planning for migratory alosids of the Atlantic

coast. Fisheries Management Report No. 6, 347 p. ASMFC, Washington, D.C. [Available from <http://www.asmfc.org/uploads/file/1985FMP.pdf>.]

<sup>12</sup>ASMFC (Atlantic States Marine Fisheries Commission). 2007. American shad stock assessment report for peer review, vol. 3. Stock Assessment Report No. 07-01 (Supplement), 489 p. ASMFC, Washington, D.C. [Available from <http://www.asmfc.org/uploads/file/2007ShadStockAssmtReportVolumeIII.pdf>.]

<sup>13</sup>ASMFC (Atlantic States Marine Fisheries Commission). 2009. Review of the Atlantic States Marine Fisheries Commission fishery management plan for shad and river herring (*Alosa* spp.) 2009, 11 p. ASMFC, Washington, D.C. [Available from <http://www.asmfc.org/uploads/file/2009ShadFMPReview.pdf>.]

## Materials and methods

### Study area

Albemarle Sound is an extensive estuarine habitat in northeastern North Carolina, measuring 88.5 km long east to west and 4.8–22.5 km wide north to south (Street et al.<sup>4</sup>; Fig. 2). Known spawning populations of Hickory Shad are located in 3 of the 15 tributaries—the Roanoke, Cashie, and Chowan Rivers—all of which are situated at the extreme western end of Albemarle Sound. The estuary is relatively shallow, with depths ranging from 5.5 to 7.6 m, and is bordered by cypress swamps and small sand beaches. The sound is essentially freshwater through its western and central portions and brackish in the eastern part. Access to the Atlantic Ocean is at Oregon Inlet between Bodie and Hatteras islands, which are parts of the Outer Banks barrier island system. The Roanoke River is the largest tributary to Albemarle Sound in terms of freshwater input. Only the last 220.5 km of the river are accessible to anadromous fishes; upriver portions are blocked by a series of impoundments ending with the Roanoke Rapids Reservoir upstream from Weldon (Rulifson and Manooch, 1991). The coastal plain portion of the watershed downstream of the last dam has an extensive floodplain that consists of hardwood forest, backwater swamps, oxbow lakes, and small creeks (Zincon and Rulifson, 1991), which are connected to the river by natural and anthropogenic openings in the natural river levee (Walsh et al., 2005).

### Field collection

Adult Hickory Shad were collected during 2 independent gillnet surveys and the Roanoke River recreational fishery. Albemarle Sound and its tributaries were sampled in the NCDMF Independent Gill Net Survey of Albemarle Sound Striped Bass from 19 February to 1 May 1996. Anchored, experimental gill nets in both floating and sinking configurations were 36.6 m long and constructed of monofilament with stretched mesh sizes ranging from 64 to 178 mm in 13-mm increments; additional nets of 203-mm and 254-mm stretched mesh were also used (Dilday and Winslow<sup>14</sup>). The lower Roanoke River at the Roanoke River National Wildlife Refuge (RRNWR; Fig. 2) was sampled during an independent gillnet survey conducted by personnel from the National Marine Fisheries Service and RRNWR from 30 March to 17 April 1996. The single-mesh gill nets ranged from 3.6 m long and 1.5 m deep to 12.2 m long and 2.3 m deep; stretched mesh sizes ranged from 63 mm to 76 mm (Settle et al., 1996). During the spawning run, fish from the sport fishery at Weldon were

obtained at access points (primarily boat ramps) and examined fresh; fish from the gillnet surveys were frozen and transported to the laboratory for examination. Each fish was measured for both FL and total length (TL) in millimeters and weighed to the nearest gram. Gonads were removed from the fresh fish and weighed to the nearest gram, and ovaries were preserved in 10% cold buffered formalin for later examination. Chi-square tests were used to determine significant differences in adult sex compositions between the 3 collection sites, and regression analyses were used to establish length-weight relationships.

### Age analysis

Both scales and sagittal otoliths were used for aging adult Hickory Shad. From the left side above the lateral line and below the dorsal fin, 10–20 scales were removed. Scales were soaked in soapy water to remove dirt, mucus, and residual pigment and then dried. For examination under a microfiche reader equipped with a 24× lens, scales were mounted between 2 glass slides. Whole otoliths were removed, then aged by placing each in a watch glass containing distilled water and viewed under a dissecting microscope at 30× magnification. Otoliths were not sectioned for aging because their thin nature allowed their rings to be visible on their external portions.

Both scales and otoliths were aged by 3 independent readers; each determination was considered successful when either the scale or otolith ages of at least 2 readers agreed. For scale aging, the traditional techniques and criteria of Cating (1953), Judy (1961), Street and Adams<sup>15</sup>, and Pate (1972) were used. Otolith aging techniques used criteria by Kornegay (1977) and Libby (1985). Results for fish aged with both scales and otoliths were used to determine agreement between the 2 aging methods.

Otoliths were used to back calculate growth because erosion of scale margins during the spawning migration precludes the necessary relationship between fish length and scale radius (DeVries and Frie, 1996). To determine the relationship of otolith radius to FL, we used 75 fish, of which all fish <250 mm FL and nearly all fish >350 mm FL; 8 of those larger fish had otoliths that were unreadable. The 2 dominant length classes (250–299 and 300–349 mm FL) were subsampled to minimize bias associated with the effect that dominant size classes can have on linear regression calculations. Otolith images were measured on a video screen connected to a dissecting microscope at 16× power; otolith annuli were measured vertically from the nucleus to the ventral margin.

<sup>14</sup>Dilday, J. L., and S. E. Winslow. 2000. North Carolina striped bass monitoring. Annual report, Grant F-56, segment 7, 43 p. [Available from Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, 3441 Arendell St., Morehead City, NC 28557.]

<sup>15</sup>Street, M. W., and J. G. Adams. 1969. Aging of hickory shad and blueback herring in Georgia by the scale method. Contribution Series No. 18, 13 p. Marine Fisheries Division, Georgia Game and Fish Commission, Brunswick, GA.

Two separate methods were used to estimate length at age. FL at age was estimated from the von Bertalanffy growth equation (Cailliet et al., 1986), which was calculated with mean back-calculated FL at age (sexes combined). Back calculations also were computed by the Dahl-Lea direct proportion method (DeVries and Frie, 1996) with the following equation:

$$L_i = (S_i / S_c) L_c, \quad (1)$$

where  $L_i$  = back-calculated FL (mm) of the fish at formation of the  $i^{\text{th}}$  increment;

$L_c$  = FL (mm) at capture;

$S_c$  = otolith radius at capture; and

$S_i$  = otolith radius at the  $i^{\text{th}}$  increment.

### Mortality estimates

Mortality was estimated for ages where recruitment was more than 95% complete (on the basis of catch curves)—for males ages 3–5, females ages 4–6, and sexes combined ages 3–6 to eliminate age classes not fully recruited to the spawning population. Total instantaneous mortality ( $Z$ ) was calculated by least-squares regression, and by estimating the slope of the line from the catch curve of a single season. Annual total mortality ( $A$ ) was estimated by taking the inverse natural log of  $-Z$  and subtracting the value from 1 (Ricker, 1975):

$$A = 1 - e^{-Z}. \quad (2)$$

### Spawning history

Spawning history for both sexes was determined by counting the number of spawning marks on the scales; spawning marks are formed by erosion of the scale margin from lack of feeding during the spawning migration (Cating, 1953; Pate, 1972). Spawning marks are thicker and more visible than the winter annuli that form before a fish matures sexually. The presence of these marks on scales is indicative of repeat spawners in a population, and the percentage of repeat spawners can be calculated. The percentage of the population that was sexually mature was calculated by sex by dividing the number of fish with developed gonads by the total number of fish examined.

### Fecundity and gonadosomatic index

When this research was completed in 1996, gonadal maturity and fecundity were not well understood. We understand now that the Hickory Shad is a batch spawner (Murauskas and Rulifson, 2011), a characteristic that requires special consideration in the estimation of fecundity (Olney et al., 2001; Murua and Sabrido-Rey, 2003). However, in 1996, sexual maturity was assigned by visual inspection of the gonads. We present the gonadosomatic index (GSI) here as documentation and for comparison with other limited studies of this species in other watersheds. For sexually mature indi-

viduals, the number of ova present in each ovary was estimated by the gravimetric method.

Each preserved whole ovary was blotted with a wet paper towel and then weighed to the nearest 0.01 g. Three subsamples of ovarian tissue, each ~0.50 g, were taken from each ovary at the anterior, medial, and posterior regions. Each subsample was weighed, the ova were counted, and the number of ova per gram of ovarian tissue was calculated. The mean number of ova present in the 3 subsamples was multiplied by ovary weight to estimate the total number of ova in that ovary; the sum of the ova in the 2 ovaries was considered the estimate of total potential fecundity. The GSI was estimated by dividing the gonad weight by somatic body weight (no gonads or gastrointestinal tract), and then multiplying the quotient by 100. The mean GSI was calculated by week so that temporal changes in the GSI could be identified. Two-sample  $t$ -tests with assumed unequal variances were used to detect differences between left and right ovaries in weight and total counts of ova. To detect significant differences in the number of ova per gram of ovarian tissue between the 3 regions of the ovary, analysis of variance was performed with Statistical Analysis System<sup>16</sup> software. Regression analysis was used to predict potential fecundity on the basis of FL, somatic weight, and age. Significance was assigned an alpha ( $\alpha$ ) value of 0.05.

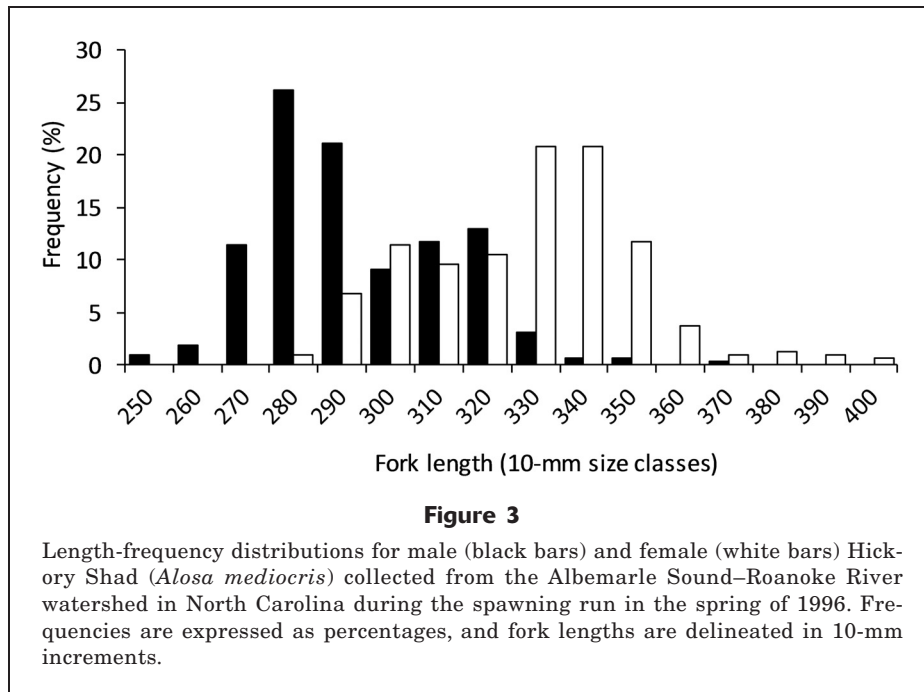
### Mesentery fat and gut content analyses

The few literature references available on this topic indicate that Hickory Shad usually do not feed during the spring spawning migration (White and Curtis<sup>17</sup>; Curtis<sup>18</sup>; Perkins and Dahlberg, 1971; Pate, 1972; Harris et al., 2007). However, we observed Hickory Shad in the Roanoke River (during this study) and Neuse River (Murauskas and Rulifson, 2011) with full stomachs, and Harris et al. (2007) found similar trends in the St. Johns River population. To determine whether feeding or fat reserves were more important during the phase of inland spawning migration, we removed mesentery fat from the viscera and weighed it to the nearest 0.01 g. Food items removed from the stomach and intestine were identified to the lowest practical taxon, enumerated, and weighed to the nearest 0.01 g.  $T$ -tests were used to test for significant differences in mesentery fat between males and females and between fish collected in Albemarle Sound and fish collected in the Roanoke River. Relationships between mesentery fat and somat-

<sup>16</sup>Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

<sup>17</sup>White, M. G., III, and T. A. Curtis. 1969. Anadromous fish survey of the Black River and Pee Dee River watersheds. Project AFS-2-4, 73 p. South Carolina Wildlife Resources Department, Charleston, SC.

<sup>18</sup>Curtis, T. A. 1970. Anadromous fish survey of the Ashley River watershed. Project AFS-2, 91 p. South Carolina Wildlife Resources Department, Charleston, SC.



ic weight and between mesentery fat and gonad weight were estimated by regression analyses.

## Results

### Sex ratios, lengths, and age

The male-to-female ratio of 0.73:1 ( $n=266$ ) for Albemarle Sound was similar ( $\chi^2=0.064$ ,  $n=532$ ,  $df=1$ ,  $P>0.05$ ) to the ratio for the spawning grounds on the Roanoke River at Weldon (0.76:1,  $n=266$ ). Although there were more female Hickory Shad collected in the Albemarle Sound than on the spawning grounds in the river, the sex ratios were similar at both areas; however, in the RRNWR, the sex ratio was significantly skewed toward males. The independent gillnet survey conducted in the RRNWR was biased by the gear characteristics used (e.g., mesh sizes), yielding a male-to-female ratio of 4.29:1 ( $n=111$ )—a value significantly different from that of the other 2 sites ( $\chi^2=54.28$ ,  $n=643$ ,  $df=2$ ,  $P<0.001$ ). The mean size and range of lengths were larger for females than for males. Females were 280–402 mm FL, and males were 257–376 mm FL. Dominant size classes (10-mm increments) were 330–339 and 340–349 mm FL for females (41.5%) and 280–289 and 290–299 mm FL for males (47.3%) (Fig. 3).

Body weight, or  $\text{Log}_e$  body weight (BWT) measured in grams, increased with length, or  $\text{Log}_e$  FL measured in millimeters, for both males (coefficient of determination [ $r^2$ ]=0.78) and females ( $r^2=0.73$ ). The following equations were used to calculate these relationships:

$$\text{Males: } \log_e BWT = 3.09(\log_e FL) - 11.76; \text{ and } \quad (3)$$

$$\text{Females: } \log_e BWT = 2.94(\log_e FL) - 10.80. \quad (4)$$

Because gonad weight varied considerably for both sexes, the length-weight relationship was calculated for somatic weight ( $\log_e SWT$ ), improving the linear fit for males ( $r^2=0.81$ ) and females ( $r^2=0.76$ ). The following equations were used to determine these relationships:

$$\text{Males: } \log_e SWT = 3.01(\log_e FL) - 11.34; \text{ and } \quad (5)$$

$$\text{Females: } \log_e SWT = 2.78(\log_e FL) - 9.98. \quad (6)$$

As expected, the relationship between FL and TL was highly correlated ( $r^2=0.99$ ). The following equation was used to establish this relationship:

$$\text{Log}_e TL = 0.99(\log_e FL) + 0.19. \quad (7)$$

Ages determined from scales and otoliths showed only a 57% agreement ( $n=478$  pairs). On the basis of results of similar otolith-scale comparisons reported for Hickory Shad (Murauskas, 2006) and for other species (e.g., Kornegay, 1977; Paramore, 1998; Paramore and Rulifson, 2001), we assumed that otolith ages were accurate. With that assumption, scales generally overestimated the age of younger fish and underestimated the age of older fish (Table 1). However, scale and otolith ages never differed by more than 2 years for any given fish. There was no agreement between age-2 scales and otoliths. Agreement of age-3 scales and otoliths was 62%, age-4 scales and otoliths had a 61% agreement, and only 26% of scales age 5 and older agreed (Table 1).

**Table 1**

Percent agreement of ages, measured in years, from scales and otoliths of Hickory Shad (*Alosa mediocris*) collected in Albemarle Sound from February to May 1996. Data represent percent agreement calculated with otolith age as the standard; bold numbers indicate one-to-one correspondence (100% accuracy).

Otolith age	Scale age						Total number of otoliths examined
	2	3	4	5	6	7	
2	<b>0</b>	65	35	0	0	0	20
3	4	<b>62</b>	30	4	0	0	242
4	0	23	<b>61</b>	15	1	0	192
5	0	15	55	<b>25</b>	5	0	20
6	0	0	0	0	<b>50</b>	50	2
7	0	0	0	0	50	<b>50</b>	2
Total number of scales examined	10	209	208	44	5	2	478

Because of the deciduous nature of *Alosa* scales, otoliths were used for age composition analyses, mortality estimates, and back calculations of length at age. Scales that agreed in age with their respective otoliths were used for spawning mark analysis.

The Hickory Shad population in the Albemarle Sound and Roanoke River ranged from age 2 to age 7, but the majority were age-3 and age-4 fish (Table 2). Age-3 males were dominant (66%), and the majority of females (55%) were age 4. Females were larger at age than were males, but size ranges (Table 2) and weights (Table 3) at age for each sex showed some degree of overlap.

There was a strong relationship between otolith radius and FL. The following equations were used to express this relationship:

$$\text{Males: } FL = 133.32(\text{otolith radius}) - 62.35, \quad (r^2 [\text{coefficient of determination}] = 0.95); \quad (8)$$

$$\text{Females: } FL = 116.54(\text{otolith radius}) - 31.18, \quad (r^2 = 0.92); \quad \text{and} \quad (9)$$

$$\text{Sexes combined: } FL = 117.02(\text{otolith radius}) - 29.20, \quad (r^2 = 0.93). \quad (10)$$

The von Bertalanffy growth equation was

$$L_t = 460 (1 - e^{-0.24(t + 163)}). \quad (11)$$

In general, the mean back calculations of length at age were shorter than the observed lengths for younger fish and longer than observed lengths for older fish (Table 2). With the proportional method, back-calculated lengths for male Hickory Shad of ages 2–4 were shorter

**Table 2**

Observed means and ranges of fork lengths at age, measured in millimeters and years, respectively, and back-calculated estimates of fork lengths at age of male and female Hickory Shad (*Alosa mediocris*) collected from the Albemarle Sound–Roanoke River watershed in 1996. Sexes combined represent the predicted size-at-age from the von Bertalanffy growth function (VBGR). Standard deviations (SD) are provided in parentheses. *n* = number of fish sampled.

Age	Males				Females				Sexes combined (VBGR)
	<i>n</i>	Mean (SD)	Range	Calculated	<i>n</i>	Mean (SD)	Range	Calculated	
1	0			206	0			212	215
2	16	293 (9.3)	278–314	247	9	304 (7.0)	292–313	263	268
3	178	288 (12.9)	257–328	287	78	313 (18.4)	280–360	306	309
4	69	319 (11.9)	283–354	293	133	339 (15.3)	296–390	345	341
5	4	332 (16.4)	318–355	355	18	343 (18.8)	320–397	363	366
6	1	376			1	402		402	386
7	0				2	397 (4.2)	394–400	394	402
Total	268				241				

**Table 3**

Observed means and ranges of body and somatic weights at age, measured in grams and years, respectively, of male and female Hickory Shad (*Alosa mediocris*) collected from the Roanoke River-Albemarle Sound watershed in 1996. Standard deviations (SD) are provided in parentheses.  $n$ =number of fish sampled.

Age	$n$	Males				$n$	Females			
		Body weight		Somatic weight			Body weight		Somatic weight	
		Mean	Range	Mean	Range		Mean	Range	Mean	Range
2	16	330 (41.7)	273-411	310 (35.8)	256-388	9	391 (27.3)	358-446	343 (15.8)	325-379
3	178	319 (54.1)	210-548	300 (57.8)	197-525	78	440 (85.4)	291-839	390 (71.1)	280-612
4	69	451 (70.2)	316-698	422 (59.8)	297-640	133	591 (101.1)	359-839	505 (83.2)	318-705
5	4	452 (65.2)	403-542	430 (69.6)	385-532	18	639 (113.9)	447-908	542 (84.6)	417-710
6	1	651		638		1	1031		871	
7						2	946 (192.0)	810-1082	779 (145.4)	676-881
Total	268					241				

and lengths for age-5 males were longer than observed values. Females were similar to males except for age-7 fish, which had back-calculated lengths that were shorter than observed values. Predicted FL values from the von Bertalanffy growth equation were less than the observed lengths for age-2 fish and greater than the observed lengths for fish of ages 5-7. Predicted lengths for age-3 and age-4 fish fell between the mean observed lengths for age-3 and age-4 males and females (Table 2). Females were larger and heavier at age than males (Tables 2 and 3).

#### Mortality, maturity, and fecundity

Mortality estimates were lower for males than for females. Total instantaneous mortality ( $Z$ ) was 1.43 for males of ages 3-5, 1.76 for females of ages 4-6, and 1.40 for both sexes combined. Annual total mortality ( $A$ ) was 0.76 for males, 0.83 for females, and 0.75 for both sexes combined. Between 36% and 38% of both male and female Hickory Shad were sexually mature by age 2, most (>93%) were mature by age 3, and almost all were mature by age 4 (Table 4). Virgin males represented 46.8% of the male population; an additional 45.5% had spawned once, and 7.7% had spawned at least 2 or more times (Table 4). No males exhibited more than 3 spawning marks. Virgin females composed only about one-fourth (24.9%) of the sample, 45.5% of females had spawned once before, and 29.1% of them showed evidence of spawning 2 or 3 times. One age-7 female had 4 spawning marks (Table 4).

Slowly increasing trends in the mean GSI were observed for Hickory Shad from both Albemarle Sound and Roanoke River through March, whereas mean GSI slowly decreased through the week of April 7-13 and then decreased quickly thereafter (Fig. 4). The mean number of ova per gram of ovarian tissue ranged from more than 1500 to less than 4000, and the anterior por-

tions of both ovaries tended to have higher ova counts per gram of ovarian tissue than the posterior region. This relationship was significant for the left ovary ( $n=47$ ,  $F=4.68$ ,  $P=0.011$ ) but not for the right ovary ( $F=1.21$ ,  $P=0.303$ ). The left ovary was significantly greater in weight and mean total egg counts than the right ovary ( $n=186$ ,  $t=3.686$ ,  $P<0.001$ ). Mean left ovary weight was 42.88 g, and mean right ovary weight was 35.98 g. Mean left egg count was 111,037, and the right ovary contained an average of 93,630 ova. These means were not significantly different for the left and right ovaries ( $n=47$ ,  $t=-1.746$ ,  $P=0.840$ ). Potential fecundity (PF) of female Hickory Shad generally increased with fish length, body weight, somatic weight, and age class (Table 5). Fecundity estimates ranged from 80,290 to 478,944 ova ( $n=47$ ). We used the following prediction equations:

$$\text{Log}_e PF = 3.90(\text{log}_e FL) - 10.46 \quad (r^2=0.63); \quad (12)$$

$$\text{Log}_e PF = 1.33(\text{log}_e BWT) + 3.70 \quad (r^2=0.76); \quad (13)$$

$$\text{Log}_e PF = 1.39(\text{log}_e SWT) + 3.59 \quad (r^2=0.67); \quad \text{and} \quad (14)$$

$$\text{Log}_e PF = 0.30(\text{Age}) + 10.97 \quad (r^2=0.52) \quad (15)$$

#### Feeding and mesentery fat

Fish collected from the Roanoke River had significantly less mesentery fat reserves than Albemarle Sound fish (males:  $n=62$ ,  $t=-3.050$ ,  $P=0.005$ ; females:  $n=110$ ,  $t=-4.54$ ,  $P<0.0001$ ). Also, male fish from the Roanoke River had significantly less remaining fat than Roanoke River females ( $n=98$ ,  $t=-2.140$ ,  $P=0.030$ ), but this sex difference was not observed for fish collected in Al-



**Table 4**

Proportion (%) of mature fish by sex, determined from visual inspection of gonads, and number of spawning marks by age class for male and female Hickory Shad (*Alosa mediocris*) collected from the Roanoke River–Albemarle Sound watershed in 1996.  $n$ =number of fish examined.

Age	Males						Females						
	Percent mature	Number of spawning marks				$n$	Percent mature	Number of spawning marks				$n$	
		0	1	2	3			0	1	2	3		4
2	36.1	12				12	38.5	7					7
3	97.9	92	56			148	93.9	38	24				62
4	99.6	4	50	14		68	98.6	6	69	48			123
5	100	1	0	1	2	4	100	2	4	9	3		18
6	100	0	0	0	1	1	100	0	0	0	1	0	1
7							100	0	0	1	0	1	2
$n$ examined	233	109	106	15	3	233	213	53	97	58	4	1	213
Proportion (%) of total population		46.8	45.5	6.4	1.3			24.9	45.5	27.2	1.9	0.5	

bemarle Sound ( $n=74$ ,  $t=-1.570$ ,  $P=-0.120$ ), indicating that both sexes feed extensively in ocean waters before entering the phase of inland spawning migration. There were weak positive relationships between somatic weight and mesentery fat for both males ( $r^2=0.17$ ) and females ( $r^2=0.29$ ) in the Albemarle Sound, but these relationships essentially disappeared (males:  $r^2=0.14$ ; females:  $r^2=0.02$ ) on the spawning grounds in the Roanoke River (Fig. 5).

Interestingly, a similar set of relationships was observed between gonad weight and mesentery fat in males and females (males:  $R^2=0.46$ ; females:  $R^2=0.21$ ) in the Albemarle Sound—relationships that disappeared (males:  $R^2=0.20$ ; females:  $R^2=0.05$ ) on the spawning grounds (Fig. 6), indicating that fish were using mesentery fat during their upstream migration for metabolic energy and not for increasing gonad size.

For gut analysis, the stomachs of 212 fish were examined. Of the fish collected from the Albemarle Sound and Roanoke River, 26% (62) and 28% (110), respectively, contained identifiable items. In fish from both locations, 83% of stomach items found fitted into 5 categories: fish (Clupeidae), parasites (Isopoda), seeds, wood, and plastic. Insects, a sixth category, were found only in stomachs of Roanoke River fish.

## Discussion

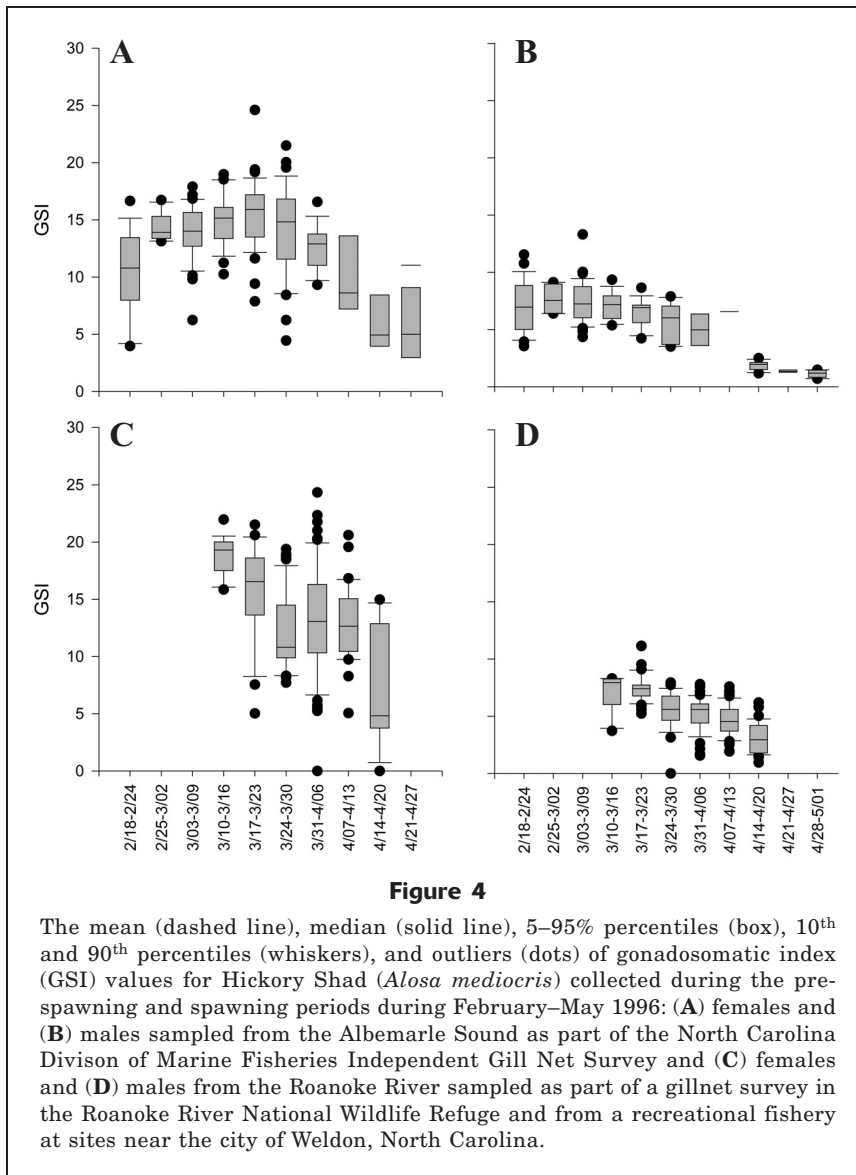
### Adult sex ratios

The sex ratios in our study indicated that there was no sex-selective harvest by anglers in 1996. The male-to-female ratios from near the Roanoke River spawning

grounds at Weldon (0.76:1) indicated that slightly more females than males were sampled. A similar result (0.73:1) was obtained from the NCDMF Independent Gill Net Survey of Striped Bass in the Albemarle Sound, but the independent gillnet survey in the RRNWR selected for male fish (4.29:1). The RRNWR survey used small mesh sizes, causing bias toward smaller males; the gillnet survey in Albemarle Sound for Striped Bass used a wide range of mesh sizes to allow for collection of the full size range of both sexes.

In some cases, males were more abundant than females because a greater proportion of males reach maturity at an earlier age; moreover, differential arrival periods of males and females on the spawning grounds, as in the Chesapeake Bay, can affect the sex ratios found in samples (Klauda et al. 1991a). Pate (1972) found the male-to-female ratio to be 4:1 for Hickory Shad sampled by a nonselective haul seine in the Neuse River, North Carolina. This ratio could have been the result of recruitment of a large proportion of virgin males to the spawning population (47.3% of the males were age 2).

Skewness of true sex ratios from increased mortality of a targeted sex likely plays a role in population rebuilding. For *Alosa* species, females are obviously the limiting factor, and older age classes have greater reproductive potential. Higher rates of survival to repeat-spawning age and a sex ratio closer to 1:1 should lead to accelerated population rebuilding, as opposed to the rebuilding potential of a population with far more males and virgin spawners. Some alosine fisheries (e.g., American Shad) target females for their roe (Rulifson et al., 1982), and such activity will shift the true sex ratio.



#### Age analysis, otolith back calculations, and mortality estimates

The 57% agreement between scale and otolith ages in our study in the Albemarle Sound–Roanoke River watershed is similar to results reported by Harris et al. (2007), who found a 57.3% agreement for fish from St. Johns River; 96% of the ages were in agreement of one year. Our study found no more than 2 years disagreement for any given fish. Kornegay (1977) reported a similar agreement for Alewife from Albemarle Sound, but for Blueback Herring his agreement was approximately 68%. Kornegay's (1977) Alewife scale ages never deviated by more than 2 years from otolith ages, but, for 2 Blueback Herring, scale ages deviated by up to 3 years from otolith ages.

A difference of 1 or 2 years between scale age and

otolith age is a relatively large deviation for a fish with a lifespan of only 7 or 8 years. Likewise, the agreement level of 57% between scale and otolith ages is low. *Alosa* scales are commonly regenerated, and spawning marks sometimes obscure annuli near the scale margin. The first annulus is sometimes confused with the freshwater zone, which is a false annulus formed when juvenile *Alosa* first enter the marine environment, and the first annulus is not always visible on the scale (Cating, 1953; Judy, 1961; Kornegay, 1977). In addition, the Hickory Shad, among *Alosa* species, has scales considered to be the most difficult to use for age analysis (Richkus and DiNardo<sup>1</sup>). Therefore, otoliths should be used whenever possible for aging Hickory Shad.

The few published studies on age composition of Hickory Shad and other *Alosa* species generally show 1–3 dominant year classes (Street and Adams<sup>15</sup>; Pate, 1972; Street et al.<sup>4</sup>; Kornegay, 1977; Winslow<sup>19,20</sup>; NCDMF<sup>21</sup>; Harris et al., 2007). In our study, ages 3 and 4 were the dominant age classes, with male Hickory Shad contributing the majority of the younger age classes (ages 2 and 3) and female Hickory Shad contributing the majority of the older age classes (ages 4–7) (Table 2). For the adjacent Neuse River, Murauskas and Rulifson (2011) reported that both sexes averaged 3 years of age, although a larger proportion of females were in older age classes: 25% of females were of ages 4, 5, and 6, whereas 14% of males were of age 4 only.

Overlapping lengths at age made it difficult to accurately determine age structure from length fre-

<sup>19</sup>Winslow, S. E. 1989. North Carolina alosid fisheries management program. Completion report for Project AFC-27, 102 p. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC.

<sup>20</sup>Winslow, S. E. 1990. Status of American Shad, *Alosa sapidissima* (Wilson), in North Carolina. Completion report for Job 5, Project AFC-27, 94 p. + appendix. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC.

<sup>21</sup>NCDMF. 2001. North Carolina shad and river herring compliance report, 2000, 66 p. [Available from Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, 3441 Arendell St., Morehead City, NC 28557.]

quencies. Other studies on Hickory Shad and other *Alosa* species also showed a significant degree of overlap of lengths at age (Street and Adams<sup>15</sup>; Pate, 1972; NCD-MF<sup>21</sup>). Our results indicate that the mean FLs at age for both sexes from age 3 and older were smaller than the means reported from earlier investigations. This difference could be the result of 1) the capture method used by previous investigators, who collected Hickory Shad in gill nets with large mesh sizes that were set for American Shad (Street et al.<sup>4</sup>; Hawkins<sup>8</sup>), 2) the scales used for determining age, or 3) both. Pate (1972) examined Hickory Shad captured in a nonselective haul seine and found that the largest Hickory Shad of both sexes were the oldest fish sampled (ages 5–7).

The mean FLs from back calculations with both the Dahl-Lea direct proportion method and the von Bertalanffy growth equation indicate that the smaller age-2 Hickory Shad were not part of the spawning migration. The largest differences between mean observed FLs and mean back-calculated FLs from the von Bertalanffy growth equation occurred at age 2 (Table 2). The only age-2 fish sampled were the ones that were sexually mature. Analysis of spawning marks showed that approximately 41% of age-2 Hickory Shad (sexes combined) were mature at this age, indicating that the majority of age-2 Hickory Shad were not sampled. It is presumed that age-1 fish and many age-2 fish remain at sea, but this portion of the lifecycle is unknown.

Annual mortality rates were higher in this study (0.75, sexes combined) than in previous studies in Albemarle Sound; rates from other studies ranged from 0.40 to 0.65 (Street et al.<sup>4</sup>; Johnson et al.<sup>22</sup>). However, it should be noted that the annual mortality in those studies was calculated with the Robson and Chapman (1961) method that computes survival instead of using the catch curve to estimate mortality. Our mortality rates were higher for females (0.83) than for males (0.76). Because the catch curve was generated from just 1 year of data, it is difficult to determine the cause for higher mortality estimates. Moderate fluctuations

<sup>22</sup>Johnson, H. B., D. W. Crocker, B. F. Holland Jr., J. W. Gilliken, D. L. Taylor, M. W. Street, J. G. Loesch, W. H. Krete Jr., and J. G. Travelstead. 1978. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. Completion Report AFCS-9-2, 175 p. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC, and Virginia Institute of Marine Science, Gloucester Point, VA.

**Table 5**

Number of ova, estimated gravimetrically and from regressions developed for age, in ovaries of female Hickory Shad (*Alosa mediocris*), collected in Albemarle Sound and the Roanoke River in 1996, and mean values of the following variables: fork length (FL) measured in millimeters, body weight (BWT) measured in grams, and somatic weight (SWT) measured in grams at age, measured in years.  $n$ =number of ovaries examined.

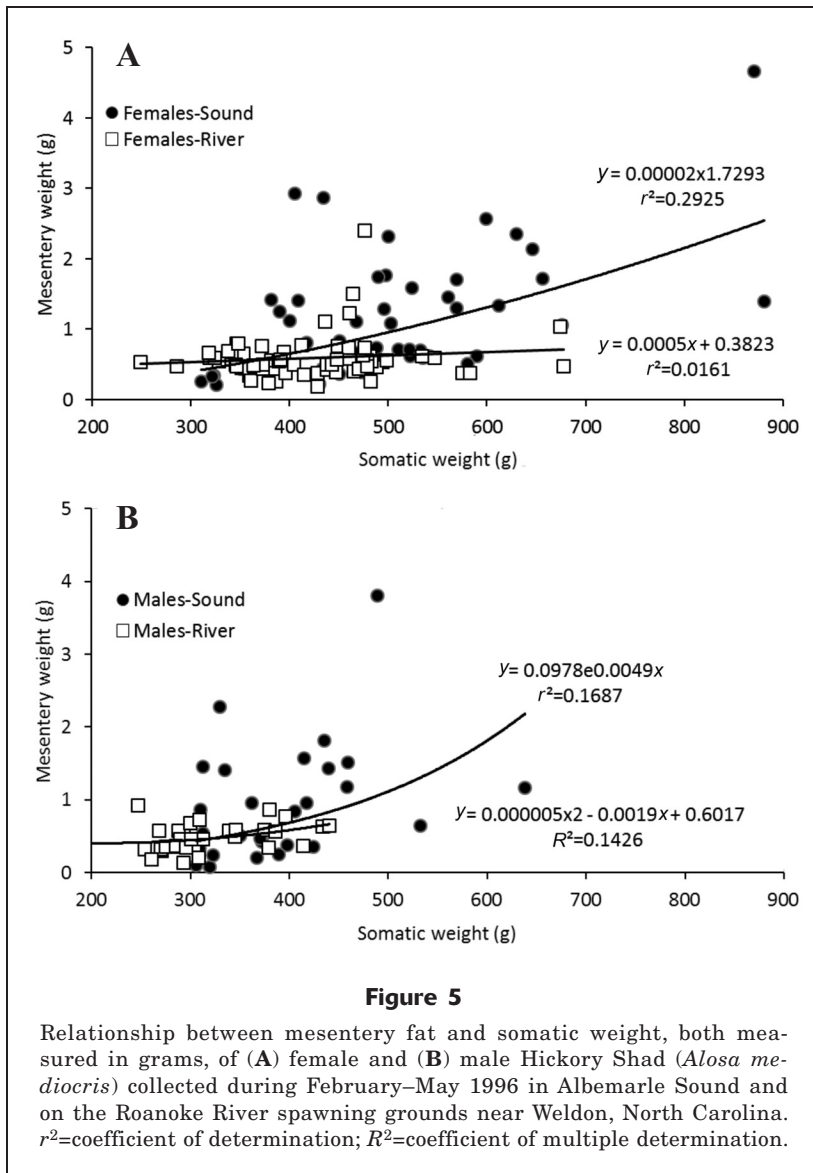
Age	$n$	Gravimetric counts (observed)	Counts on basis of age	Counts by mean FL at age	Counts by mean BWT at age	Counts by mean SWT at age
2	1	85,803	108,012	138,195	113,366	121,109
3	14	137,523	147,267	154,849	132,642	144,776
4	19	223,576	200,787	211,380	196,382	207,344
5	3	294,798	273,758	221,275	217,874	228,758
6	1	478,944	373,249	410,929	411,646	442,326
7	2	250,918	508,897	391,352	367,134	378,751

in annual recruitment are common in fish populations, but catch curves derived from 2 or more years of data can reduce the effects of variable recruitment (Ricker, 1975).

#### Spawning history and reproductive analysis

The short lifespan of Hickory Shad, combined with an early age to maturity and an anadromous migration pattern, indicates that adult fish in the Albemarle Sound–Roanoke River population are subject to recreational (sound and inland waters) and commercial harvest (sound and ocean waters) for 1 or 2 seasons before they are removed by harvest or natural mortality. Approximately one-third of both sexes are sexually mature as early as age 2, >93% of the population is mature by age 3, and essentially 100% of the population is mature by age 4 (Table 4). One or 2 spawning marks on the scales examined were common, but 3 or more marks were rare. These results were similar to findings for Hickory Shad in the Altamaha River, Georgia (Street, 1970), the Neuse River (Pate, 1972), and more recently the Tar-Pamlico River (Murauskas and Rulifson, 2011).

On the basis of age to maturity and spawning patterns, Hickory Shad and American Shad are exploited similarly in the Albemarle Sound region, but the level of exploitation for these species differs south of Cape Hatteras. American Shad in Albemarle Sound usually reach sexual maturity by age 3 or age 4 for males and by age 4 or age 5 for females. Both sexes spawned up to 3 times (Winslow<sup>19,20</sup>). American Shad show a latitudinal gradient between semelparity and iteroparity throughout its range (Leggett and Carscadden, 1978). In contrast, individual American Shad in populations south of Cape Hatteras seldom spawn more than once, and adults in populations in New York and Connecticut



spawn up to 5 times. Hickory Shad appear to be iteroparous south of Cape Hatteras as indicated by repeat spawners in the Neuse River (Pate, 1972; Hawkins<sup>8</sup>), Altamaha River (Street, 1970), and St. Johns River (Harris et al., 2007). Because of the short life spans and limited number of spawning events (i.e., repeat spawning) exhibited by Hickory Shad and other *Alosa* species, successive years of poor recruitment could result in relatively quick population declines. Therefore, our estimate of 0.75 for annual total mortality, sexes combined, is possible. State landings data for Hickory Shad after 1996 indicate that such a mortality estimate may have been real (Fig. 1). Landings stabilized in the 2000s decade.

Mean GSI values were similar between fish caught in the Albemarle Sound and fish captured in the Roanoke River. The spawning season for Hickory Shad in

the Albemarle Sound–Roanoke River watershed lasts for about 4 weeks in March and April; therefore, female Hickory Shad will be at differing degrees of gonadal development (i.e., pre-spawning, running ripe, partially spent, postspawning) for any given week during the spawning season, and this variation will result in a large variability in GSI values (Fig. 4). Murauskas and Rulifson (2011) observed multiple batch spawning of Hickory Shad in the Tar-Pamlico River watershed over several weeks, and these events were related to water temperature. This observation is supported by our ovary data, which revealed significantly different states of maturity between anterior and posterior oocytes in the ovaries.

Fecundity estimates are important in population modeling and also for hatchery managers who attempt to spawn and rear Hickory Shad for the purpose of stock restoration. The Maryland Department of Natural Resources has been rearing and stocking larval and early juveniles of both Hickory Shad and American Shad in at least 6 Chesapeake Bay watersheds and tributaries (Richardson et al.<sup>23</sup>). Although Olney et al. (2001) and Murauskas and Rulifson (2011) classified both species as batch spawners, Maryland hatchery personnel do not mention this aspect in their methodology. Both males and females received an intramuscular implant of leutinizing-hormone-releasing hormone analog (LHRHa) in the dorsal musculature at the collection site and were returned to the hatchery for spawning. Very little information exists on fecundity estimates of Hickory Shad, and estimates include age-2 fish. Pate (1972) reported 44,556 to 347,610 eggs per female from the Neuse River. Hickory Shad in the Altamaha River showed increased fecundity with age and size, with estimates ranging from 252,693 to 730,213 eggs per female and a mean of 500,519 eggs per female (Street, 1970). St. Johns River females exhibited low correlation between fecundity and weight, length, and age. Fecundity ranged from 168,000 to 591,000 eggs per female with a mean of 363,000 eggs per female (Williams and Bruger<sup>9</sup>). Our study of the Roanoke River population (egg counts from

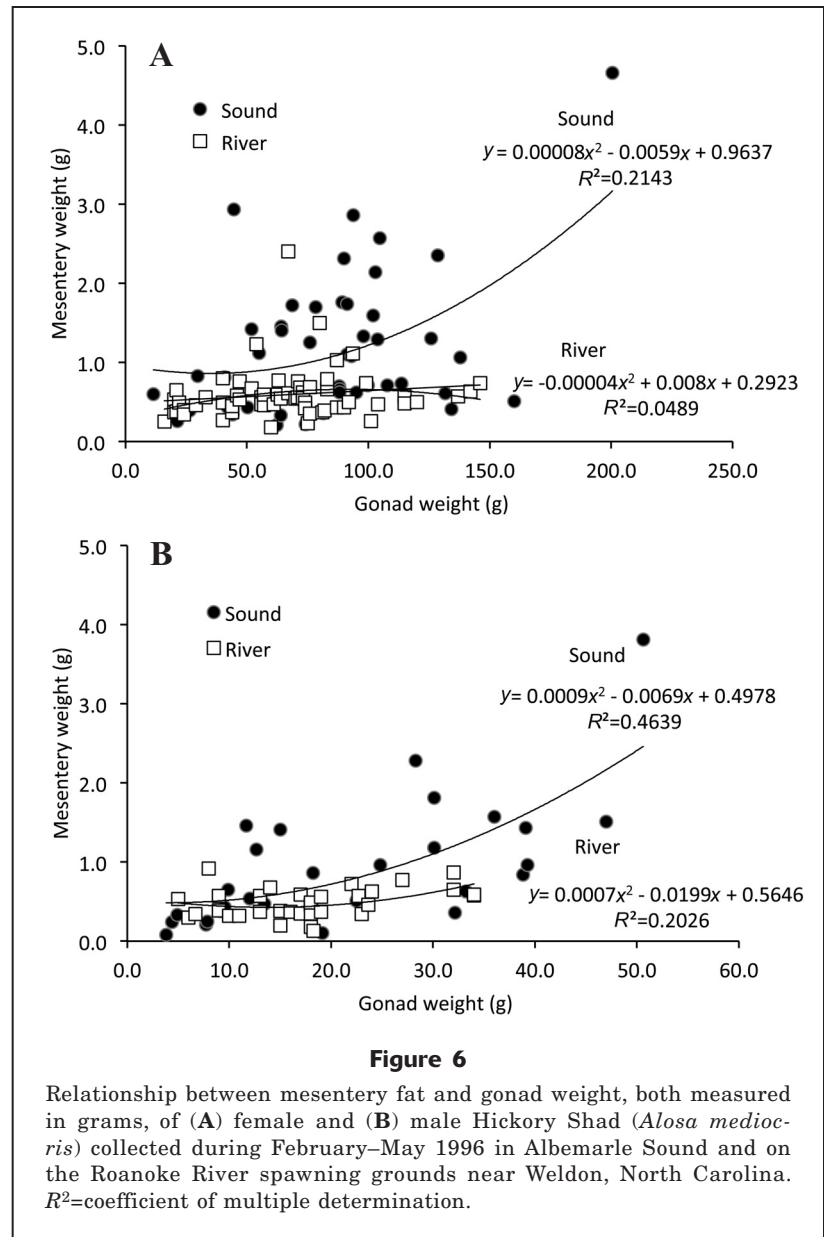
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<sup>23</sup>Richardson, B. M., C. P. Stence, M. W. Baldwin, and C. P. Mason. 2009. Hickory shad restoration in three Maryland rivers. F-57 Segment 9 Progress Report, 48 p. Maryland Department of Natural Resources, Oxford, MD. [Available from <http://www.dnr.state.md.us/irc/docs/00014544.pdf>.]

80,290 to 478,944) found good correlation of egg counts with weight, length, and age (Table 5).

It appears that suitable spawning habitats differ among watersheds. Spawning activity of Hickory Shad in the Neuse River, North Carolina, and the Altamaha River, Georgia, was confined primarily to flooded bottomlands and tributaries away from the main stem of each river (Street, 1970; Pate, 1972; Burdick and Hightower, 2006). Smith (2006) noted Hickory Shad spawning in small tributaries of the Tar-Pamlico River watershed. Mansueti (1962) found Hickory Shad spawning in the main stem of the Patuxent River, Maryland, upstream of American Shad spawning sites. Hickory Shad have been found to spawn in both the main stem and tributaries of rivers in Virginia (Klauda et al., 1991b). In the Roanoke River upstream of our study area, Harris and Hightower (2011) conducted a study of spawning habitat for Hickory Shad, and they determined that adults generally avoided spawning in areas with very low (<0.1 m/s) or no water velocity, especially when substrate sizes were small. When water velocities were low (<0.1 m/s), spawning occurred only on bedrock substrates. When water velocities were higher ( $\geq 0.1$  m/s), spawning occurred on a variety of substrate types, including gravel and occasionally sand. Although we did not survey spawning habitat of Hickory Shad in the Roanoke River in 1996, both ripe and partially spent adults were collected from tributaries of the Roanoke River in the RRN-WR and at Weldon. The higher flows of the Roanoke River in the spring flood the backwater tributaries and swamps; therefore, maintenance of a flow regime similar to the natural springtime flows probably is needed to ensure suitable spawning habitat for Hickory Shad in this watershed.

Why spawning runs of Hickory Shad in the 1990s far exceeded the spawning runs of American Shad in the Roanoke River–Albemarle Sound watershed remains a mystery. Historically, American Shad dominated harvests of anadromous shad in every major watershed in mid-Atlantic and South Atlantic states. Near the turn of the 20th century in 1890, North Carolina landings of American Shad totaled 2.616 million kg (5.768 million lb), increasing to 4.066 million kg (8.963 million lb) in 1897 and dropping to 2.979 million kg (6.567 million lb) in 1902 (Alexander, 1905). Hickory Shad landings were only 104,780 kg (231,000 lb) in 1897 and 310,711



kg (685,000 lb) in 1902. At the end of the 20th century (in 1996, the year of our study), commercial harvests of both species were nearly equal: 90,554 kg (199,638 lb) of American Shad and 85,244 kg (187,887 lb) of Hickory Shad (NCDMF database, <http://portal.ncdenr.org/web/mf/statistics/comstat>; Fig. 1). Interpretation of landings beyond 1996 becomes more difficult because the species was declared a game fish in inland waters, and harvest restrictions were subsequently put in place for the recreational fishery. How this designation of a game fish may have affected commercial harvest is unknown.

The Roanoke River fishery, once dominated by thriving commercial fisheries that targeted anadromous species American Shad, Alewife, Blueback Herring, and

Striped Bass, is now a multimillion-dollar recreational fishery best known for Striped Bass and Hickory Shad (McCargo et al.<sup>7</sup>). Habitat loss and fragmentation, along with overharvesting the species, are considered major factors in the reduction of alosine stocks to remnant populations in this watershed (Walsh et al., 2005; McCargo et al.<sup>7</sup>) and elsewhere in the North Atlantic (Limburg and Waldman, 2009). Restoration of the American Shad population in the Roanoke River has been ongoing since 1988 (Waters<sup>24</sup>), but adult abundance remains low despite the stocking of 43 million American Shad fry in the Roanoke River as of 2010 (Dockendorf<sup>10</sup>).

Populations of Hickory Shad in upper Chesapeake Bay tributaries are experiencing resurgence and are supporting an active catch-and-release recreational fishery. This resurgence also means better access to brood fish for hatchery programs, and the state of Maryland now has implemented stock restoration efforts for Hickory Shad in 3 rivers: the Patuxent, Choptank, and Nanticoke (Richardson et al.<sup>23</sup>). Maryland agencies hope to establish increased fishing opportunities for targeting Hickory Shad, believing that restoration of this species has the potential to occur over a shorter time frame (because of its earlier age at maturity) than the period needed for American Shad restoration (Richardson et al.<sup>23</sup>).

## Conclusions

Our findings clearly indicate that the short lifespan of the Hickory Shad, combined with an early age to maturity and an anadromous migration pattern, means that adult individuals of the population will be subjected to recreational and commercial harvest in inland waters for 1 or 2 seasons before they are removed by exploitation or natural mortality. Our data were collected before the implementation of the 10-fish bag limit on shads. North Carolina fisheries agencies hope that a daily 10-fish limit for shads (only 1 fish can be American Shad in the Roanoke River) will protect current population size while maintaining the interest of fishermen in this lucrative fishery. The study presented here is the most recent on this species for North Carolina; data collected during creel surveys by the NCWRC have included only recorded catches but not samples for lengths, weights, or age. We recommend that new data be collected on age and growth since this regulation went into effect to determine whether incidences of repeat spawning events have increased in this population. This growing population has a sex ratio slightly dominated by females both in the prespawning staging area in Albemarle

Sound in January and on the spawning grounds in the Roanoke River. Continued research on the poorly understood life history of this species will increase our understanding and, perhaps, provide insight on its success in relative abundance compared with that of American Shad.

## Acknowledgments

We thank the staff of the North Carolina Division of Marine Fisheries, especially H. Johnson, S. Trowell, S. Winslow, and field technicians of the Elizabeth City office for their assistance in fish collections; the National Marine Fisheries Service (Beaufort Laboratory, Southeast Fisheries Science Center) sampling crew headed by D. Peters; and the staff of the Roanoke River National Wildlife Refuge led by J. Holloman. P. Kornegay of the North Carolina Wildlife Resources Commission provided the 1996 Hickory Shad recreational harvest data for the Roanoke River. C. Manooch III, and J. Potts of the Beaufort Laboratory assisted with otolith preparation and reading. We thank K. Dockendorf, W. Patrick, J. Murauskas, A. Dell'Apa, C. Bangle, and the anonymous referees for critical review of the manuscript. Funding was provided, in part, by the North Carolina Fishery Resource Grant program (through the NC Marine Fisheries Commission), Project No. M-6057, to R. Rulifson.

## Literature cited

- Alexander, A. B.  
1905. Statistics of the fisheries of the South Atlantic states, 1902, 67 p. Division of Statistics and Methods of the Fisheries, U.S. Fish Commission. GPO, Washington, D. C.
- Batsavage, C. F.  
1997. Life history aspects of the hickory shad (*Alosa mediocris*) in the Albemarle Sound/Roanoke River watershed, North Carolina. M.S. thesis, 100 p. East Carolina Univ., Greenville, NC.
- Burdick, S. M., and J. E. Hightower.  
2006. Distribution of spawning activity by anadromous fishes in an Atlantic Slope drainage after removal of a low-head dam. *Trans. Am. Fish. Soc.* 135:1290-1300.
- Cailliet, G. M., M. S. Love, and A. W. Ebeling.  
1986. Fishes: a field and laboratory manual on their structure, identification, and natural history, 194 p. Wadsworth Publ., Belmont, CA.
- Cating, J. P.  
1953. Determining age of Atlantic shad from their scales. *Fish. Bull.* 54:187-199.
- DeVries, D. R., and R. V. Frie.  
1996. Determination of age and growth. *In* Fisheries techniques, 2nd ed. (B. R. Murphy and D. W. Willis, eds.), p 483-508. Am. Fish. Soc., Bethesda, MD.
- Harris, J. E., R. S. McBride, and R. O. Williams.  
2007. Life history of hickory shad in the St. Johns River, Florida. *Trans. Am. Fish. Soc.* 136:1463-1471.

<sup>24</sup>Waters, C. T. 2000. Summary of activities in 1998 and 1999 for restoring American Shad to Roanoke River. [Available from North Carolina Wildlife Resources Commission, 1751 Varsity Dr., Raleigh, NC 27606.]

- Harris, J. E., and J. E. Hightower.  
2010. Evaluation of methods for identifying spawning sites and habitat selection for alosines. *N. Am. J. Fish. Manage.* 30:386–399.  
2011. Spawning habitat selection of hickory shad. *N. Am. J. Fish. Manage.* 31:495–505.
- Judy, M. H.  
1961. Validity of age determination from scales of marked American shad. *Fish. Bull.* 61:161–170.
- Klauda, R. J., S. A. Fischer, L. W. Hall, and J. A. Sullivan.  
1991a. Alewife and blueback herring. In *Habitat requirements for Chesapeake Bay living resources*, 2<sup>nd</sup> ed. (S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley, eds.), p 10–1–10–29. Chesapeake Research Consortium, Solomons, MD.  
1991b. American Shad *Alosa sapidissima* and Hickory Shad *Alosa mediocris*. In *Habitat requirements for Chesapeake Bay living resources*, 2<sup>nd</sup> ed. (S. L. Funderburk, J. A. Mihursky, S. J. Jordan, and D. Riley, eds.), p 9–1–9–27. Chesapeake Research Consortium, Solomons, MD.
- Kornegay, J. W.  
1977. A comparison of the scale and otolith methods of ageing alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*). M.S. thesis, 79 p. East Carolina Univ., Greenville, NC.
- Leggett, W. C., and J. E. Carscadden.  
1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. *J. Fish. Res. Board Can.* 35:1469–1478.
- Libby, D. A.  
1985. A comparison of scale and otolith aging methods for the alewife, *Alosa pseudoharengus*. *Fish. Bull.* 83:696–701.
- Limburg, K. E., and J. R. Waldman.  
2009. Dramatic declines in North Atlantic diadromous fishes. *Bioscience* 59:955–965.
- Manooch, C. S., III.  
1984. Fisherman's guide to fishes of the southeastern United States, 362 p. North Carolina State Museum of Natural History, Raleigh, NC.
- Mansueti, R. J.  
1962. Eggs, larvae, and young of the hickory shad, *Alosa mediocris*, with comments on its ecology in the estuary. *Chesapeake Sci.* 3:173–205.
- Marshall, M. D.  
1977. Status of hickory shad in North Carolina. In *Proceedings of a workshop on American shad had* (R. St. Pierre, ed.), p. 33–45. U.S. Fish and Wildlife Service and National Marine Fisheries Service, Amherst, MA.
- Melvin, G. D., M. J. Dadswell, and J. D. Martin.  
1986. Fidelity of American shad, *Alosa sapidissima* (Clupeidae), to its river of previous spawning. *Can. J. Fish. Aquat. Sci.* 43:640–646.
- Murauskas, J. G.  
2006. Investigating the reproductive migration of adult hickory shad, *Alosa mediocris*. M.S. thesis, 121 p. East Carolina Univ., Greenville, NC.
- Murauskas, J. G., and R. A. Rulifson.  
2009. A comprehensive approach to understanding diadromy at the species level: learning from the spawning migration of hickory shad. In *Challenges for diadromous fishes in a dynamic global environment* (A. Haro, K. L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, Michael J. Dadswell, R. A. Cunjak, J. E. Cooper, K. L. Beal, and T. S. Avery, eds), p. 837–840. *Am. Fish. Soc. Symp.* 69, Bethesda, MD.  
2011. Reproductive development and related observations during the spawning migration of hickory shad. *Trans. Am. Fish. Soc.* 140:1035–1048.
- Murua, H., and F. Saborido-Rey.  
2003. Female reproductive strategies of marine fish species of the North Atlantic. *J. Northwest Atl. Fish. Sci.* 33:23–31.
- Olney, J. E., S. C. Denny, and J. M. Hoenig.  
2001. Criteria for determining maturity stage in female *Alosa sapidissima* and the mystery of partial spawning. *Bull. Fr. Peche Piscic.* 362/363:881–901.
- Paramore, L. M.  
1998. Age, growth, and life history characteristics of striped bass, *Morone saxatilis*, from the Shubenacadie-Stewiacke River, Nova Scotia. M.S. thesis, 91 p. East Carolina Univ., Greenville, NC.
- Paramore, L. M., and R. A. Rulifson.  
2001. Dorsal coloration as an indicator of different life history patterns for striped bass within a single watershed of Atlantic Canada. *Trans. Am. Fish. Soc.* 130:663–674.
- Pate, P. P.  
1972. Life history aspects of the hickory shad, *Alosa mediocris* (Mitchill), in the Neuse River, North Carolina. M.S. thesis, 66 p. North Carolina State Univ., Raleigh, NC.
- Perkins, R. J., and M. D. Dahlberg.  
1971. Fat cycles and condition factors of Altamaha River shads. *Ecology* 52:359–362.
- Ricker, W. E.  
1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191, 382 p.
- Robins, C. R., G. C. Ray, and J. Douglass.  
1986. A field guide to Atlantic Coast fishes of North America, 354 p. Houghton Mifflin, Boston, MA
- Robson, D. S., and D. G. Chapman.  
1961. Catch curves and mortality rates. *Trans. Am. Fish. Soc.* 90:181–189.
- Rulifson, R. A.  
1994. Status of anadromous *Alosa* along the East Coast of North America. In *Anadromous Alosa symposium, Tidewater Chapter*. (J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, eds.), p. 134–158. *Am. Fish. Soc.*, Bethesda, MD.
- Rulifson, R. A., and C. S. Manooch, III (eds.).  
1991. Roanoke River Water Flow Committee report for 1990. NOAA Tech. Memo. NMFS-SEFEC-291, 433 p.
- Rulifson, R. A., M. T. Huish, and R. W. Thoesen.  
1982. Anadromous fish in the southeastern United States and recommendations for development of a management plan, 525 p. U.S. Fish and Wildlife Service, Atlanta, GA.
- Smith, M. C.  
2006. Habitat use of early *Alosa* spp. and striped bass, *Morone saxatilis*, in the lower Tar River, North Carolina. M.S. thesis, 165 p. East Carolina Univ., Greenville, NC.
- Street, M. W.  
1970. Some aspects of the life histories of hickory shad, *Alosa mediocris* (Mitchill), and blueback herring, (*Alosa aestivalis*) (Mitchill), in the Altamaha River, Georgia. M.S. thesis, 89 p. Univ. Georgia, Athens, GA.

- Walberg, C. H.  
1960. Abundance and life history of the shad, St. Johns River, Florida. *Fish. Bull.* 60:487-501.
- Waldman, J. R., and K. E. Limburg.  
2003. The world's shads: summary of their status, conservation, and research needs. *In* Biodiversity, status, and conservation of the world's shads (K. E. Limburg and J. R. Waldman, eds.), p. 363-369. *Am. Fish. Soc. Symp.* 35, Bethesda, MD.
- Walsh, H. J., L. R. Settle, and D. S. Peters.  
2005. Early life history of blueback herring and alewife in the lower Roanoke River, North Carolina. *Trans. Am. Fish. Soc.* 134:910-926.
- Watkinson, E. R.  
2004. Age, growth, and fecundity of hickory shad (*Alosa mediocris*) in a Virginia coastal river. M.S. thesis. Virginia Commonwealth Univ., Richmond, VA.
- Zincone, L. H., and R. A. Rulifson.  
1991. Instream flow and striped bass recruitment in the lower Roanoke River, North Carolina. *Rivers* 2:125-137.