

1 **The Anadromous Hickory Shad (Clupeiformes: Clupeidae, *Alosa mediocris* [Mitchill**
2 **1814]): Morphometric and Meristic Variation**

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4 Jordan P. Smith, Department of Biology, East Carolina University, Greenville, NC 27858
5 Michael S. Brewer, Department of Biology, East Carolina University, Greenville, NC 27858
6 Roger A. Rulifson, Department of Biology, East Carolina University, Greenville, NC 27858

7
8 Author contact: rulifsonr@ecu.edu
9

10 **Abstract**

11 The anadromous Hickory Shad *Alosa mediocris* (Mitchill, 1814) (Clupeiformes:
12 Clupeidae) is reviewed, specifically regarding morphometric and meristic variation. Despite its
13 long history as recognized species, few descriptions of Hickory Shad morphometric and meristic
14 characters exist in the literature. Most authors of the historic literature have failed to provide
15 capture location for specimens, analyze large numbers of Hickory Shad, or document how
16 morphometric and meristic characters of the species vary spatially. To address this information
17 gap, a total of 717 mature Hickory Shad were collected from 23 different locations in Maryland,
18 Delaware, Virginia, North Carolina, South Carolina, Georgia, and Florida using electroshocking,
19 gill net, or rod and reel. All specimens were frozen, thawed, and 17 morphometric characters and
20 four meristic characters were examined; a random subset (n = 463) were analyzed for an
21 additional four meristic counts of gill rakers. Overall specimens ranged from 206-389 mm SL
22 with a mean \pm SD of 278.41 ± 27.69 mm, 232-435 mm FL with a mean of 310.98 ± 30.35 mm,
23 and 272-508 mm TL with a mean of 365.62 ± 35.52 mm. The linear relationships between FL
24 and TL, and FL and SL, were investigated and found to be: $TL = 1.169*FL + 1.660$ (n=705,
25 $r^2=0.995$) and $SL = 0.909*FL - 4.274$ (n=717, $r^2=0.992$). Substantial differences in character
26 means for many morphometric measurements were found between male and female specimens,
27 suggesting strong sexual dimorphisms relating to shape. However, meristic characters did not
28 show differences in character means by sex. No one morphometric measurement could
29 distinguish Hickory Shad from other morphologically similar clupeids, but the meristic count of
30 gill rakers on the lower limb of the first arch were important to separate Hickory Shad (19-22)
31 from American Shad *A. sapidissima* (Wilson, 1811), Alewife *A. pseudoharengus* (Wilson, 1811),
32 and Blueback Herring *A. aestivalis* (Mitchill, 1814).
33

34 **Introduction**

35 No published study has examined and described an extensive set of morphometric and
36 meristic characters of the Hickory Shad *Alosa mediocris* (Mitchill, 1814) (Clupeiformes:
37 Clupeidae). The initial description of Hickory Shad lacked some critical information, indicating
38 that this was a species unknown to the system and proceeded to describe it from “fresh
39 specimens.” Unfortunately there is no reference to the capture location of the fish nor quantity

40 examined. It is possible that the description could have been based from one or several
41 individuals. We speculate that the likely watershed from which Mitchill collected his
42 specimen(s) was the Hudson River due to its close proximity to Columbia University.

43 Few records exist of Mitchill's early attempts to describe New York fauna, including *A.*
44 *mediocris*. Perhaps Professor Mitchill took students to the shores of the Hudson River to observe
45 fauna from pulling small seines; unless more early writings of Professor Mitchill are discovered,
46 the locations and manner of these ichthyological collections will remain unknown. One or more
47 of those specimens collected was an undescribed species of "Shad", which he presumably took
48 back to his laboratory for examination and decided the specimen(s) fit within the family
49 Clupeidae. Mitchill proceeded to designate the species *Clupea mediocris* – the "Staten Island
50 Herring". In a presumably similar manner, Mitchill also described 11 other new species during
51 that era (including what is now known as *Alosa aestivalis* (Mitchill, 1814), the Blueback
52 Herring) although all 12 new "Mitchillian" species, including the current-day Hickory Shad and
53 Blueback Herring, were placed in different genera by subsequent authorities [1].

54 Unfortunately, the original description of the Hickory Shad contained only a sparse
55 description of the anatomical features. Mitchill [2] included basic descriptions of the fish shape,
56 color, size, and meristic counts for branchiostegal, pectoral, ventral, anal, dorsal, and caudal fin
57 rays, but he did not include any information on morphological measurements or ratios of size
58 between various body features. Interestingly, many researchers describing the few characteristics
59 of this species did so citing other investigators, who in turn cited Mitchill [2]. Therefore, little
60 additional meristic or morphological information has been recorded for the species since the
61 original description, over 200 years ago.

62 In addition, no record can be located of the holotype, nor where or when the specimen
63 was collected. During this time of budding taxonomy in America, it was neither common nor
64 required to keep holotype specimens for newly described species. Other taxonomists after
65 Mitchill revised the taxonomic status of the Hickory Shad. Notably, the genus *Alosa* was divided
66 into three genera by Regan [3] in 1917: *Alosa*, *Caspialosa*, and *Pomolobus*; the Hickory Shad
67 was classified under the genus *Pomolobus* along with the Alewife and the Blueback Herring [4].
68 Later work by Bailey [5] and Svetovidov [6] led to synonymizing the genera *Pomolobus* and
69 *Caspialosa* with the genus *Alosa*, thereby changing the scientific name of Hickory Shad from
70 *Pomolobus mediocris* to *A. mediocris* (Mitchill, 1814) [4].

71 Mansueti [7] examined the hypothesis that the Hickory Shad might be a hybrid between
72 the American Shad *Alosa sapidissima* (Wilson, 1811) and one of the River Herrings, the Alewife
73 *Alosa pseudoharengus* (Wilson, 1811) or the Blueback Herring *A. aestivalis*. He concluded that
74 hybridization was unlikely and “not substantiated by any reliable evidence” [7]. Around this
75 time, a few fish culturists experimented in hatcheries and actively pursued creating hybrids
76 involving Hickory Shad and River Herring, though none of these attempts were successful [7].

77 The objective of this manuscript is to fully describe the various anatomical features,
78 including meristic counts and morphological measurements, of the Hickory Shad across its
79 range. The Hickory Shad is considered an understudied fish species though it spawns in rivers on
80 the United States Eastern Seaboard from the Schuylkill River in the Delaware River watershed
81 [8] to the St. Johns River in Florida [9]. The northern range limit of Hickory Shad spawning
82 populations is not precisely known; early authors hypothesized spawning as far north as Maine
83 [10]. A spawning population is suspected in Wethersfield Cove in the Connecticut River near
84 Wethersfield, Connecticut, but evidence is lacking; adult Hickory Shad have been collected from

85 that area during spring (Ken Sprankle, USFWS, personal communication). Rulifson [11]
86 reported that Connecticut is the northernmost state having a presence of Hickory Shad based on
87 responses to questionnaires by respective state fisheries biologists. It is possible some of these
88 northern accounts of Hickory Shad are either misidentifications with morphologically similar
89 species, such as the American Shad *A. sapidissima*, or possibly wandering Hickory Shad
90 collected in bays or the Atlantic Ocean, but not actively spawning. The Hickory Shad is a
91 schooling species of the family Clupeidae and utilizes the life history strategy of anadromy,
92 entering coastal freshwater between February and June to spawn; the higher latitudes correspond
93 to later dates of entry into freshwater [12].

94 Relatively few authors have included morphometric and meristic values for Hickory Shad
95 [13], [14], [15], [10], [16], [17], [18] but none investigated how these characters vary spatially.
96 Most previous studies fail to provide capture location(s) for the specimens examined and cover
97 many fewer characters than the present study. Furthermore, some authors provide only one value
98 for various meristic counts and morphometric measurements, when in reality there is often
99 considerable variation. No published study has described Hickory Shad specimens across such a
100 large latitudinal gradient, covering the majority of the species range. Similar studies have been
101 undertaken for the American Shad [19], Alewife, and Blueback Herring [20].

102 Historically, morphometric and meristic analyses of fish have been valuable tools for
103 early ichthyologists and naturalists alike [21]. Starting in 1894, the Royal Society of the United
104 Kingdom created the “Committee for Conducting Statistical Inquiries into the Measurable
105 Characters of Plants and Animals.” One of the committee’s chief tasks was to investigate
106 morphometric variation in Atlantic Herring *Clupea harengus* (Linneaus, 1758) [22]. Analysis of

107 morphological and meristic characters of fish is straightforward, cost-efficient, and an often-used
108 tool to identify and differentiate fish species, stocks, and populations [23].

109

110 **Methods**

111

112 Hickory Shad specimens were collected during the 2016 and 2017 spawning runs from
113 the Susquehanna and Patapsco rivers, Maryland; the Nanticoke River, Delaware; the
114 Rappahannock, Appomattox, and James rivers, Virginia; the Chowan River headwaters
115 (Meherrin, Nottaway, and Blackwater), also in Virginia; the Roanoke, Cashie, Pungo, Pamlico,
116 Tar, Neuse, New, and Cape Fear rivers, North Carolina; Pamlico Sound, also in North Carolina;
117 the Waccamaw and Santee rivers, South Carolina; the Altamaha River, Georgia, and the St.
118 Johns River, Florida (Table 1). In addition, a few specimens (n=5) were obtained from the
119 Atlantic Ocean close to shore, near Wrightsville Beach, North Carolina. Relative location of
120 rivers as well as collection sites are depicted in Figure 1. All specimens were collected from the
121 different locations by recreational angling (i.e., rod and reel), gill net, or electrofishing.
122 Specimens from rivers outside of North Carolina were collected and donated to this study by the
123 respective state or federal fisheries agencies. North Carolina fish came from the North Carolina
124 Wildlife Resources Commission (NCWRC) or the North Carolina Division of Marine Fisheries
125 (NCDMF). Additional sampling was conducted by the Rulifson Lab with electrofishing and rod
126 and reel (NC Scientific Collection Permit Number 17-SFC00133; East Carolina University AUP
127 #D330).

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Table 1. List of states and river (north to south), sex, and total number of Hickory Shad collected in 2016 and 2017.

State	River	Sex			Total
		Female	Male	Unknown	
Maryland	Susquehanna R.	13	9		22
Maryland	Patapsco R.	11	39		50
Delaware	Nanticoke R.	16	6		22
Virginia	Rappahannock R.	23	21	3	47
Virginia	Appomattox R.	25	25		50
Virginia	James R.	26	37	2	65
Virginia	Chowan R. (Meherrin)		1		1
Virginia	Chowan R. (Nottaway)	7	11		18
Virginia	Chowan R. (Blackwater)	13	11	1	25
North Carolina	Roanoke R.	21	23		44
North Carolina	Cashie R.	17	17		34
North Carolina	Pamlico Sound	63	29	2	94
North Carolina	Pungo R.		2	1	3
North Carolina	Pamlico R.	39	24	1	64
North Carolina	Tar R.	31	20	1	52
North Carolina	Neuse R.	14	30	3	47
North Carolina	New R.	2	2	6	10
North Carolina	Atlantic Ocean*	3		2	5
North Carolina	Cape Fear R.	5	13		18
South Carolina	Waccamaw R.	7			7
South Carolina	Santee R.	2	4		6
Georgia	Altamaha R.	26	4		30
Florida	St. Johns R. (Wekiva)	1	2		3
		365	330	22	717

*denotes non-river or sound sampling location

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132 Figure 1. Map showing relative location of rivers included in this study as well as collection sites
 133 of Hickory Shad. Revised after Melvin et al. [28].

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135 Initially all specimens were frozen in water to minimize freezer burn and fin breakage,

136 and then eventually transferred to the Rulifson Lab at East Carolina University (ECU) for

137 examination. Once received or collected, fish were identified to species based on projection of

138 the lower jaw beyond the maxilla (as opposed to the American Shad, for which the lower jaw

139 inserts into a slot in the maxilla), weighed to the nearest 0.01 g, bagged individually without
140 water, and given a unique identification number. After this step the fish were placed in freezers (-
141 20°C or -0°C) on the ECU campus until analysis. Specimens were removed from the freezer and
142 slowly allowed to thaw. A small tissue sample was taken from the dorsal fin, which was then
143 placed in 95% ethanol (ETOH) and stored in a -80°C freezer for later genetic analysis.

144 A total of 17 morphometric measurements and 4 meristic characters (Table 2) were
145 recorded generally following the methods outlined by Hubbs and Lagler [24]. All measurements
146 were straight line distances from point to point on the left side of the body unless there was
147 physical damage: standard length (SL) -- distance between most anterior portion of the head
148 (lower jaw) to the last vertebrae; fork length (FL) -- the distance between the lower jaw to the
149 fork of the caudal tail; total length (TL) -- the greatest distance between lower jaw and end of
150 caudal fin when the caudal rays are pinched together; lower lip to nose (LLN) -- the distance of
151 the projecting lower jaw to maxilla; snout to anal length (SAL) -- the distance between lower jaw
152 and the anus; body depth (BD) -- greatest depth distance between anterior to dorsal fin and
153 anterior of the ventral fin; head length (HL) -- the distance from lower jaw to the most distant
154 point of the operculum (including membrane); eye length (EL) -- the greatest distance of the
155 orbit; snout length (SNL) -- the distance from the most anterior point of the upper lip to the
156 anterior margin of the orbit; head width (HW) -- the distance (width) across the head where the
157 preopercle ends; interorbital width (IOW) -- distance between the eyes at the top of the cranium;
158 maxillary length (ML) -- the distance from the tip of the upper jaw to the distal end of the
159 maxillary; fin length dorsal base (FLD) -- the greatest distance of the structural base between the
160 origin and insertion of the dorsal fin when the fin is erect; fin length anal base (FLA) -- the
161 greatest distance of the structural base between the origin and insertion of the anal fin when the

162 fin is erect; longest ray dorsal fin (LRD) -- the distance from the structural base of the dorsal fin
163 to the tip of the longest ray; longest ray pectoral fin (LRP) -- distance from the structural base of
164 the pectoral fin to the tip of the longest ray; longest ray ventral (pelvic) fin (LRV) -- distance
165 from the structural base of the ventral fin to the tip of the longest ray; longest ray anal fin (LRA)
166 -- distance from the structural base of the anal fin to the tip of the longest ray when the fin is
167 erect. A Hickory Shad illustration (Figure 2) depicts how most morphometric measurements
168 were taken. IOW and HW were omitted on the illustration since they are width measurements
169 and cannot be accurately depicted. The standard length, total length, and snout-to-anal length
170 were measured to the nearest mm; all other measurements were taken by using Fisherbrand
171 “Traceable” digital calipers (model number 06-644-16) to the nearest 0.01 mm.
172

Table 2. Morphometric measurements and meristic counts analyzed, and acronyms used in this study.

Morphometric	Acronym	Meristic	Acronym
Standard Length	SL	Posterior Ventral Scutes	PVS
Fork Length	FL	Anterior Ventral Scutes	AVS
Total Length	TL	Scale Rows	SR
Lower Lip-Nose	LLN	Longitudinal Scale Rows	LSR
Snout-to-Anal Length	SAL	Left Gill Raker Upper	L-GRU
Body Depth	BD	Right Gill Raker Upper	R-GRU
Head Length	HL	Left Gill Raker Lower	L-GRL
Eye Length	EL	Right Gill Raker Lower	R-GRL
Snout Length	SNL		
Head Width	HW		
Interorbital Width	IOW		
Maxillary Length	ML		
Fin Length-Dorsal Base	FLD		
Fin Length-Anal Base	FLA		
Longest Ray Dorsal Fin	LRD		
Longest Ray Left Pectoral Fin	LRP		
Longest Ray Left Ventral Fin	LRV		
Longest Ray Anal Fin	LRA		

173 Figure 2. Hickory Shad illustration showing how morphometric measurements were taken.
174 Reproduced from Whitehead [34].
175

176 External meristic counts were taken on the left side of the body, unless there was damage:
177 post ventral (pelvic) scutes (PVS) -- count of scutes from the end of the ventral fin to the anus;
178 anterior ventral scutes (AVS) -- count of scutes from the beginning of the operculum to the
179 ventral fin, including the scute straddling the ventral fins; scale rows (SR) -- count of scales
180 along the lateral line, beginning at the upper angle of the operculum and terminating at the end of
181 the hypural plate as determined with a crease in the caudal peduncle by folding the tail; and
182 longitudinal scale rows (LSR) -- count of scales from the origin of the dorsal fin to the origin of
183 the ventral fin. A random subset of specimens (n = 463) were analyzed for an additional four
184 internal meristic counts, including the left and right gill rakers of the upper first arch (L-GRU, R-
185 GRU) -- count of all gill rakers on the upper arch of first gill raker, not including the raker
186 straddling the angle; and left and right gill rakers lower (L-GRL, R-GRL) -- count of all first arch
187 gill rakers from the raker straddling the angle to the end, regardless of size.

188 External meristic characters including the scale rows between the upper angle of gill
189 opening and base of caudal fin, longitudinal scale rows between origin of ventral fin and origin
190 of dorsal fin, post-ventral scutes, and anterior-ventral scutes, were all counted from the freshly-
191 thawed specimens.

192 To the best of our knowledge, there are no references in the literature detailing specific
193 methods for counting scutes of clupeids. We chose to divide the scute count into two -- anterior
194 and posterior -- of the ventral fin following Smith [17], though Nichols [26] and Melvin et al.
195 [19] chose to count total scutes for American Shad. All scutes were counted, regardless of size,
196 from where the ventral surface reaches the operculum posterior to the anus. Special care was

197 given to check for scutes obscured by the anus in all fish, specifically ripe females. Occasionally
198 scales near the scutes had to be removed to fully expose all scutes, and then counts were obtained
199 with the aid of a probe.

200 After external morphometric measurements and meristic counts were completed, fish
201 were then dissected to remove the gonads, which were weighed to the nearest 0.01 g. Sex was
202 determined for each specimen based on visual inspection of the gonad. Once features of each
203 specimen were recorded, the data were compiled into one Microsoft Excel file for analyses.

204 Sample sizes for each state, watershed, and capture location were not uniform, nor were
205 the number of males and females the same, due to the various collection methods and availability
206 at the time of collection. In addition, the number of fish analyzed for each character was not
207 always equal because some of the specimens were damaged necessitating the omission of one or
208 more characters. Also the timing of the collection for each watershed was not standardized;
209 spawning often started prior to the typical timeline for state agency spring sampling. The
210 morphometric and meristic data presented here are from frozen and thawed -- not fresh --
211 Hickory Shad and for purposes of the analyses we assumed that any bias caused by this process
212 was equal across all specimens.

213

214 **Results**

215 Overall 717 Hickory Shad were analyzed for 17 morphometric measurements and four
216 meristic characters from 23 different rivers and estuaries in Maryland, Delaware, Virginia, North
217 Carolina, South Carolina, Georgia, and Florida following the methods outlined above. Results of
218 descriptive statistics for all locations combined, separated by sex, for all measurements and
219 counts are presented in Table 3. Results for each individual river and combined sex can be found

220 in Table 4. The random subset of specimens (n = 463) analyzed for four internal meristic gill
 221 raker counts showed that Hickory Shad had between 8-11 rakers on L-GRU, 8-12 rakers on R-
 222 GRU, and 19-22 rakers on both L-GRL and R-GRL.
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Table 3. Descriptive data of morphometric and meristic characters for female and male specimens of Hickory Shad. See text for descriptions of each measurement or count. All measurements given in mm.

Female						Male					
Character	Range	Mean	SD	% SL	n	Character	Range	Mean	SD	% SL	n
SL	229 - 389	292.41	26.09	-	365	SL	206 - 344	264.62	20.63	-	330
FL	260 - 435	326.36	28.57	111.61	365	FL	232 - 382	295.81	22.64	111.78	330
TL	306 - 508	383.36	33.55	131.10	364	TL	272 - 444	347.67	26.48	131.38	326
LLN	2.44 - 7.90	3.93	0.73	1.34	365	LLN	2.39 - 7.39	3.60	0.54	1.36	327
SAL	172 - 289	218.99	20.26	74.89	364	SAL	155 - 251	197.51	15.45	74.64	330
BD	65.74 - 134.89	91.44	13.32	31.27	365	BD	60.70 - 105.09	79.03	7.46	29.86	329
HL	64.73 - 108.43	81.40	6.96	27.84	364	HL	58.86 - 93.96	74.72	5.99	28.24	329
EL	11.82 - 19.60	14.80	1.26	5.06	363	EL	11.53 - 18.59	13.96	1.16	5.28	330
SNL	15.93 - 27.84	20.75	1.84	7.10	363	SNL	15.13 - 24.76	19.07	1.63	7.21	330
HW	23.67 - 47.07	31.33	3.38	10.71	363	HW	21.87 - 37.11	28.45	2.53	10.75	330
IOW	10.38 - 20.90	14.52	1.77	4.96	364	IOW	9.56 - 20.75	13.35	1.60	5.05	329
ML	26.51 - 41.90	33.98	2.52	11.62	362	ML	25.38 - 37.15	31.51	2.18	11.91	330
FLD	33.97 - 63.41	63.41	4.80	21.69	365	FLD	29.66 - 52.89	39.77	3.74	15.03	329
FLA	37.80 - 68.23	49.00	4.65	16.76	363	FLA	32.43 - 62.17	44.65	4.15	16.87	328
LRD	29.88 - 55.12	39.77	3.99	13.60	364	LRD	24.63 - 45.91	36.23	3.32	13.69	327
LRP	43.10 - 77.09	55.42	5.32	18.95	363	LRP	38.84 - 64.67	50.83	4.45	19.21	330
LRV	23.76 - 46.09	34.90	3.29	11.93	362	LRV	23.80 - 39.84	31.97	2.88	12.08	330
LRA	14.61 - 26.59	19.74	2.33	6.75	360	LRA	13.13 - 23.60	17.99	1.89	6.80	326
SR	49 - 56	51.65	1.23		349	SR	49 - 56	51.60	1.12		316
LSR	15 - 19	17.81	0.55		339	LSR	15 - 19	17.71	0.60		309
PVS	14 - 18	15.86	0.75		361	PVS	14 - 18	15.88	0.72		326
AVS	17 - 23	21.35	0.84		363	AVS	18 - 24	21.39	0.79		329

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Table 4. Morphometric and meristic characters of Hickory Shad by river of collection (north to south). For each character; minimum - maximum, and mean values are presented.

Character	Susquehanna	Nanticoke	Patapasco	Rappahannock	Appomattox	James	Meherrin	Nottaway	Blackwater	Roanoke	Cashie	Pungo
SL	234 - 318	257 - 325	249 - 309	257 - 336	234 - 300	221 - 331	265	224 - 306	233 - 334	221 - 334	234 - 326	234 - 268
FL	277.27	293.64	271.06	294.34	272.24	272.91	272.91	270.72	273.08	273.77	286.06	250.33
	260 - 353	285 - 361	281 - 347	288 - 373	263 - 336	250 - 369	302	252 - 341	266 - 375	249 - 369	266 - 368	264 - 302
	306.64	325.50	304.44	327.83	304.54	305.17	302	303.72	306.84	305.86	320.59	282.67
TL	302 - 414	336 - 421	328 - 403	338 440	310 - 395	294 - 431	353	298 - 401	311 - 441	292 - 425	315 - 433	312 - 354
	359.00	382.14	356.62	385.11	357.34	357.89	353	357.56	361.44	359.44	376.73	332
LLN	2.44 - 5.20	3.07 - 4.74	3.22 - 4.24	2.93 - 5.77	2.52 - 4.17	2.92 - 5.07	3.84	3.06 - 4.23	3.27 - 4.79	2.45 - 5.66	2.83 - 5.26	2.75 - 3.81
	3.63	4.00	3.79	4.10	3.35	3.70	3.77	3.65	3.77	3.46	3.74	3.28
SAL	171 - 234	186 - 243	188 - 235	190 - 255	175 - 227	167 - 254	202	169 - 228	171 - 256	165 - 249	176 - 251	176 - 198
	203.82	216.36	204.32	218.98	202.38	204.23	202	204.22	205.96	204.14	216.56	187.33
BD	63.79 - 94.86	71.55 - 97.23	70.19 - 93.96	75.72 - 114.74	65.74 - 97.68	66.19 - 111.24	77.60	66.58 - 101.63	69.49 - 101.80	61.29 - 101.53	67.12 - 112.66	69.22 - 77.97
	81.93	83.29	81.41	91.34	80.71	84.00	77.94	84.23	84.19	80.74	87.4	74.32
HL	65.45 - 90.54	72.56 - 89.36	70.13 - 86.79	73.19 - 94.29	67.35 - 86.34	64.42 - 91.91	77.94	65.27 - 83.91	66.72 - 92.33	62.15 - 87.45	68.15 - 90.30	67.93 - 75.88
	76.79	81.43	76.24	82.60	77.41	77.03	77.94	76.66	76.69	76.09	80.04	71.69
EL	12.61 - 17.27	13.46 - 17.25	12.75 - 15.80	13.34 - 17.54	12.31 - 15.41	11.59 - 17.74	13.97	13.11 - 15.31	13.84	12.12 - 16.34	12.97 - 15.93	12.97 - 14.53
	15.03	15.46	13.76	15.60	14.21	14.14	13.97	14.19	13.84	14.22	14.46	13.77
SNL	15.84 - 23.29	18.39 - 23.58	16.85 - 21.66	18.53 - 25.24	17.47 - 22.72	16.74 - 23.30	19.28	16.45 - 21.64	16.51 - 24.56	16.23 - 22.60	16.85 - 23.11	17.82 - 19.08
	19.51	21.22	18.84	21.24	20.14	19.92	19.28	19.56	19.36	19.49	20.03	18.32
HW	24.64 - 34.82	27.52 - 34.63	25.74 - 31.43	27.64 - 36.87	25.37 - 33.31	24.34 - 36.74	28.81	24.1 - 33.62	24.75 - 35.57	22.46 - 34.08	24.56 - 34.78	25.44 - 29.82
	29.96	31.33	28.12	31.94	29.47	29.59	28.81	29.36	29.11	29.18	30.13	27.52
IOW	12.06 - 18.16	12.87 - 16.93	12.42 - 15.79	12.62 - 18.27	12.24 - 16.32	10.59 - 17.96	13.08	10.62 - 14.96	10.31 - 14.94	10.28 - 16.64	10.84 - 15.37	10.93 - 14.28
	14.98	15.24	13.85	15.06	14.09	13.49	13.08	12.91	12.58	13.54	13.34	12.45
ML	26.57 - 37.15	30.79 - 37.94	29.36 - 35.82	29.84 - 38.15	29.04 - 35.73	27.02 - 38.54	32.79	29.53 - 35.75	28.78 - 37.48	26.1 - 36.92	29.36 - 37.59	28.70 - 30.97
	31.95	34.12	31.73	34.13	32.42	32.27	32.79	32.63	32.49	32.02	33.46	30.15
FLD	34.69 - 50.47	37.64 - 53.39	34.91 - 46.14	37.61 - 51.80	34.33 - 48.28	34.13 - 50.23	37.77	33.20 - 45.75	35.92 - 56.08	31.98 - 49.50	37.71 - 50.84	37.15 - 41.03
	41.71	45.14	39.77	45.18	41.17	41.02	37.77	40.73	41.33	41.33	43.39	38.48
FLA	38.03 - 57.49	44.93 - 55.16	35.26 - 52.49	43.73 - 57.52	38.93 - 51.78	37.22 - 53.10	43.73	37.09 - 50.92	39.43 - 53.58	37.20 - 54.42	40.05 - 55.36	41.30 - 48.69
	47.47	49.76	44.82	49.65	46.33	45.81	43.73	44.71	45.78	46.29	47.57	44.28
LRD	30.11 - 44.06	33.48 - 46.83	32.52 - 41.97	32.49 - 46.91	31.97 - 40.93	30.02 - 44.94	37.99	24.63 - 41.36	31.43 - 42.87	25.13 - 43.85	31.82 - 45.91	35.25 - 36.79
	37.67	39.04	37.38	39.85	36.76	37.02	37.99	36.18	37.07	35.96	38.54	36.23
LRP	41.66	48.74	46.33 - 57.53	48.69 - 64.12	44.77 - 57.83	41.35 - 64.92	52.07	44.70 - 58.36	45.27 - 64.07	41.38 - 59.11	47.17 - 62.22	48.18 - 51.50
	51.47	53.90	51.25	55.77	52.31	52.16	52.07	52.54	52.98	52.14	54.5	49.36
LRV	26.76 - 37.51	28.84 - 39.37	24.76 - 36.35	30.42 - 40.12	23.76 - 36.53	23.80 - 40.60	32.61	25.86 - 36.49	28.82 - 40.54	26.26 - 37.53	28.79 - 39.33	29.95 - 31.72
	32.61	34.54	32.17	35.64	33.35	32.92	32.61	32.52	33.36	32.80	34.21	30.68
LRA	14.53 - 22.32	16.36 - 21.59	13.84 - 20.94	16.35 - 23.90	14.61 - 23.35	14.44 - 23.99	19.16	15.76 - 22.11	15.25 - 23.07	14.60 - 23.53	16.18 - 23.60	17.34 - 18.26
	18.55	18.99	17.44	19.63	17.98	18.38	19.16	18.80	18.93	18.27	19.66	17.79
SR	51 - 55	52 - 55	49 - 52	50 - 56	50 - 53	50 - 56	51	50 - 52	50 - 53	51 - 55	51 - 54	50 - 52
	53.00	53.14	50.73	52.51	51.60	51.83	51	51.33	51.56	52.11	51.65	51
LSR	15 - 19	17 - 19	16 - 18	16 - 19	17 - 19	17 - 19	18	16 - 18	17 - 19	17 - 19	17 - 19	17
	18.00	17.73	17.74	18.02	17.88	17.94	18	17.61	17.92	17.73	18	17
PVS	15 - 17	15 - 18	15 - 17	15 - 17	15 - 17	14 - 17	15	14 - 17	15 - 17	15 - 17	15 - 18	15
	15.71	16.05	16.08	15.81	15.59	15.83	15	15.83	15.96	16.14	16.33	15
AVS	20 - 22	21 - 22	18 - 23	17 - 23	21 - 23	20 - 24	24	21 - 23	21 - 23	18 - 23	21 - 23	22
	21.05	21.23	21.21	21.34	21.38	21.34	24	21.61	21.50	21.59	21.56	22
n	22	22	50	47	50	65	1	18	25	44	34	3

231

232

Table 4 continued. Morphometric and meristic characters of Hickory Shad by river of collection (north to south). For each character, minimum - maximum, and mean values are presented.

Character	Pamlico	Pamlico Sound	Tar	Neuse	New	Cap Fear	Atlantic Ocean	Waccamaw	Santee	Altamaha	Wekiva	Grand Total
SL	232-361	216-349	206-375	230-330	209-279	234-333	243-313	350-389	243-354	255-365	315-344	206-389
	284.58	272.93	267.31	267.49	248.00	268.39	272.20	359.86	281.00	321.33	325.33	278.41
FL	260-402	243-393	232-417	258-363	234-312	261-371	275-350	389-435	272-394	286-406	348-382	232-435
	315.09	305.60	299.31	297.64	278.30	300.94	305.80	399.86	315.50	359.47	360.00	310.98
TL	305-472	288-460	272-487	301-427	274-369	306-436	324-413	445-508	323-464	340-479	412-444	272-508
	370.81	358.91	352.63	350.51	330.75	354.20	359.20	466.43	372.67	423.57	423.33	365.62
LLN	2.64-7.89	2.85-4.83	2.47-5.55	2.7-5.34	2.64-3.65	2.87-4.58	3.23-3.73	3.97-6.03	2.39-3.66	3.26-4.88	4.03-4.55	2.39-7.89
	4.48	3.61	3.73	3.70	3.15	3.65	3.52	4.47	2.96	3.89	4.30	3.76
SAL	174-272	166-271	155-281	172-240	158-210	174-251	182-231	257-289	182-255	194-279	229-251	155-289
	212.16	204.61	200.50	198.30	184.70	200.56	203.00	267.14	209.33	242.73	238.33	208.12
BD	65.13-124.05	65.97-106.01	60.7-121.04	63.55-111.30	60.95-91.72	73.25-110.60	70.74-85.62	125.57-134.89	74.85-114.13	77.92-126.67	100.25-103.00	60.7-134.89
	89.68	82.08	83.11	80.53	74.38	84.43	76.54	128.58	87.40	110.53	101.48	85.21
HL	61.03-91.40	61.79-103.08	58.86-105.97	62.00-93.12	60.33-80.19	67.53-91.84	69.81-88.54	93.27-108.43	68.2-94.59	71.43-101.47	85.66-93.96	58.86-108.43
	76.74	77.03	76.37	75.06	70.29	76.70	79.27	98.25	79.67	88.90	88.83	78.02
EL	11.78-19.60	11.53-17.93	11.71-18.66	11.65-17.78	11.24-14.56	11.68-15.71	12.02-14.86	16.32-18.51	12.50-17.39	12.90-17.73	15.57-17.29	11.24-19.60
	14.62	13.93	14.11	14.25	12.95	13.35	13.56	17.17	14.68	15.56	16.37	14.38
SNL	16.58-27.03	15.13-27.84	15.25-25.70	16.60-22.91	15.47-20.37	16.46-22.88	15.93-22.08	23.31-26.81	16.70-24.30	17.92-25.05	22.06-24.76	15.13-27.84
	20.59	19.27	19.59	19.38	17.52	18.59	19.40	24.69	20.15	21.59	23.03	19.90
HW	24.91-47.07	22.72-39.21	21.87-42.18	23.88-35.00	21.51-30.44	23.75-34.77	24.22-31.63	39.06-42.41	27.37-38.21	28.09-37.84	34.63-37.11	21.51-47.07
	32.09	28.21	29.05	28.75	25.88	28.32	28.13	40.62	31.30	34.10	35.49	29.86
IOW	10.84-20.90	9.59-20.42	9.56-18.25	11.00-17.11	10.49-14.32	11.29-16.73	10.93-15.89	17.09-19.73	12.83-17.51	13.42-18.29	15.69-19.44	9.56-20.90
	15.05	13.12	12.94	13.50	12.24	13.52	13.33	18.09	14.69	16.16	17.28	13.92
ML	27.00-40.51	26.51-41.23	25.38-41.78	26.92-36.81	26.05-33.92	27.86-37.37	28.99-35.74	38.93-41.90	29.55-38.37	30.43-39.79	35.43-37.15	25.38-41.90
	33.28	32.13	32.24	31.66	29.95	31.91	32.03	39.78	33.18	36.33	36.09	32.72
FLD	34.16-55.88	30.34-52.33	29.95-61.11	29.66-50.86	29.70-42.66	33.97-47.30	36.89-48.09	54.32-63.41	39.06-51.82	38.97-57.88	43.56-52.89	29.66-63.41
	42.98	41.08	40.03	39.39	37.15	40.39	41.46	56.55	43.34	49.90	49.47	42.00
FLA	35.15-60.78	35.33-56.26	32.43-62.29	36.44-53.82	36.39-50.97	39.33-56.15	41.25-54.32	55.23-68.23	40.21-63.03	37.50-64.81	56.84-62.17	32.43-68.23
	47.42	46.10	44.67	44.79	43.13	46.25	46.71	60.17	48.14	53.90	58.98	46.85
LRL	31.67-55.12	29.88-47.24	27.09-48.73	28.43-45.81	25.49-39.65	29.57-42.92	32.58-41.35	44.32-53.94	33.18-50.27	34.85-50.25	44.92-45.82	24.63-55.12
	40.38	37.10	37.22	37.08	34.72	37.38	36.74	47.71	39.95	43.37	45.32	38.01
LRLP	38.83-69.67	43.12-67.21	39.22-70.87	41.60-64.11	39.93-57.00	45.11-62.10	45.65-59.48	63.38-77.09	46.59-72.86	49.15-68.44	60.08-64.67	38.83-77.09
	53.29	52.15	51.90	50.89	47.95	52.76	51.88	69.32	56.07	61.49	61.75	53.09
LRLV	26.67-43.48	25.12-43.07	24.49-43.28	25.75-40.06	23.99-33.80	26.78-38.25	29.10-38.04	39.25-46.09	29.76-41.98	24.87-43.45	36.84-39.84	23.76-46.09
	33.55	32.59	32.44	32.28	29.71	33.03	32.51	42.80	34.64	38.01	37.93	33.40
LRA	13.13-26.34	14.16-25.17	13.79-25.80	13.99-22.77	14.08-19.09	14.30-21.19	15.88-19.85	23.49-26.59	15.11-24.14	16.79-26.33	21.40-22.86	13.13-26.59
	19.65	18.42	19.06	18.48	16.89	18.30	18.16	24.81	18.76	21.85	22.16	18.85
SR	49-55	50-55	50-54	50-54	50-52	50-51	50-51	51-53	51-52	49-52	52	49-56
	52.03	51.34	51.40	51.81	50.89	50.78	50.40	51.43	51.17	50.23	52.00	51.62
LSR	15-19	16-18	17-18	16-19	18	18	17-18	16-19	17-18	17-18	16-19	15-19
	17.51	17.63	17.79	17.36	18.00	18.00	17.60	17.86	17.67	17.67	17.33	17.77
PPS	14-18	15-17	14-17	14-17	14-17	14-17	15-16	14-16	16	14-17	15-16	14-18
	16.13	15.82	15.72	15.96	15.33	15.39	15.40	15.29	16.00	15.50	15.67	15.87
APS	17-23	20-23	20-23	19-23	21-22	21-22	21-22	21-22	21-22	20-22	21-23	17-24
	20.63	21.42	21.40	21.60	21.30	21.72	21.40	21.43	21.33	21.33	22.33	21.37
n	64	94	52	47	10	18	5	7	6	30	3	717

233

234

235 A basic review of the morphometric and meristic data showed sexual difference in many
236 characters, namely morphometric measurements. All morphometric characters showed sexual
237 difference in character means, yet some character differences were more substantial. For
238 example, the mean measurements (mm) of BD (Female: 91.44, Male: 79.03), FLD (Female:
239 63.41, Male: 39.77), SAL (Female: 218.99, Male: 197.51), and HL (Female: 81.40, Male: 74.72)
240 were largely different between sexes. For meristic counts on SR, LSR, PVS, and AVS there was
241 no observed difference between sexes and so the averages between males and females were
242 similar. Of the four counts, the largest difference in the averages was found for the count of LSR
243 where the averages were 17.81 and 17.71 for females and males, respectively. Due to the
244 differences in some characters (i.e., morphometric) by sex, it was necessary to divide the
245 morphometric and meristic data for males and females for accurate description and analysis.

246

247 Specimen Size

248 All Hickory Shad collected and included in this study were adults (sexually mature)
249 participating in the annual spawning run and all morphometric and meristic data reported are for
250 adult fish. Male specimens from locations combined ranged from 206 to 344 mm SL with a
251 mean \pm SD of 264.42 ± 20.52 mm. Female specimens ranged from 229 to 389 mm with a mean
252 of 289.72 ± 24.71 mm. Sizes for sexes and locations combined ranged from 206 to 389 mm SL
253 with a mean of 276.53 ± 26.31 mm. The linear relationships between FL and TL, and FL and SL,
254 were:

255
$$TL = 1.169*FL + 1.660 \text{ (n=705, } r^2=0.995\text{); and}$$

256
$$SL = 0.909*FL - 4.274 \text{ (n=717, } r^2=0.992\text{)}.$$

257 The largest Hickory Shad were from the Waccamaw River, SC and the mean \pm SD was
258 359.86 \pm 13.92 mm SL with a range between 350 and 389 mm SL; average weight was 1281.13
259 \pm 95.46 g and all seven specimens from this river were female. On average the smallest Hickory
260 Shad were collected from the New River, NC with a mean \pm SD of 248 \pm 24.92 mm SL and a
261 range of 209 to 279 mm SL. However, the smallest Hickory Shad collected in this study (206
262 mm SL) was a male from the Tar River, NC. Specimen total body weight (n = 695) with sexes
263 and locations combined ranged from 206.03 to 1488.28 g with a mean \pm SD of 501.34 \pm 187.52
264 g, and gonad weights (n = 691) from 0.38 to 266.03 g with a mean of 49.88 \pm 45.78 g.

265

266 Sex

267 Overall, females were larger than males of similar SL. The smallest male weighed 206.03
268 g and largest weighed 866.50 g. The smallest female weighed 242.40 g and largest 1488.28 g.
269 Gonads for females weighed from 0.38 to 266.03 g with a mean \pm SD of 74.43 \pm 51.15 g.
270 Gonads for males weighed from 0.90 to 62.53 g with a mean of 22.86 \pm 11.53 g. Variation in
271 size and weight of female gonads were largely dependent on spawning status. Some gonad
272 specimens had deteriorated so gonad weight measurements (n = 4) and sex determination (n =
273 22) were not possible. In addition, the sexing of some specimens was omitted on the data sheet
274 during the examination process.

275

276 Missing data

277 Some of the 717 Hickory Shad could not be analyzed for the entire suite of 17
278 morphometric and four meristic characters due to specimen damage. This resulted in 146 missing
279 values across all morphometric and meristic characters. Missing value analysis was performed in

280 SPSS version 24 [27] and the meristic character LSR had the most missing data (7.7%). Of the
281 remaining characters only SR, LRA, and PVS had more than 1.0% missing: 4.3, 1.3, and 1.1%,
282 respectively. Values for count and percent missing of each character are reported in [Table 5](#).
283
284
285

Table 5. Missing value analysis of 18 morphometric and four meristic characters of Hickory Shad.

Character	N	Mean	Std. Deviation	Missing	
				Count	Percent
SL	717	278.41	27.69	0	0.0
FL	717	5.73	0.01	0	0.0
TL	710	5.89	0.01	7	1.0
LLN	714	1.31	0.14	3	0.4
SAL	716	5.33	0.02	1	0.1
BD	716	4.43	0.09	1	0.1
HL	715	4.35	0.03	2	0.3
EL	714	2.66	0.05	3	0.4
SNL	715	2.98	0.04	2	0.3
HW	715	3.39	0.04	2	0.3
IOW	715	2.62	0.07	2	0.3
ML	714	3.48	0.03	3	0.4
FLD	716	3.73	0.05	1	0.1
FLA	713	3.84	0.05	4	0.6
LRD	713	3.63	0.10	4	0.6
LRP	715	3.97	0.04	2	0.3
LRV	714	3.50	0.04	3	0.4
LRA	708	2.93	0.07	9	1.3
SR	686	51.62	1.17	31	4.3
LSR	662	17.77	0.58	55	7.7
PVS	709	15.86	0.73	8	1.1
AVS	714	21.36	0.81	3	0.4

286

287

288 Comparison between Hickory Shad and other Clupeids

289 Morphometric and meristic results of this study were compared to available literature
290 values for morphologically similar clupeids, including the American Shad, Alewife, and
291 Blueback Herring (Table 6). Characters mentioned here represent the clearest difference between
292 species: Hickory Shad have a larger body depth as a percent of total length (22.31-26.55)
293 compared to American Shad (17.2-19.4) and Alewife (17.8-21.7), but body depth is similar to
294 that of Blueback Herring (22.1-25.2). The upper portions of the variable ranges for Hickory Shad
295 scute and scale row counts (PVS, AVS, and SR) were less than that for American Shad, but LSR
296 was greater for Hickory Shad. This is not surprising since the body depth as a percent of total
297 length was greatest for Hickory Shad, and the LSR character is counted along the depth of the
298 body. The range of interorbital width (IOW) as a percent of head length for Hickory Shad
299 (16.24-19.28) was most similar to Alewife (15.7-21.6); the range for American Shad (18.6-21.6)
300 was higher than for Hickory Shad but within the range for Alewife. Overall, Blueback Herring
301 interorbital width as a percent of head length (21.1-26.4) is the largest. As for eye length as a
302 percent of head length, the Hickory Shad has the smallest range (18.08-19.10), which is much
303 less than that of American Shad (27.3-32.0), Blueback Herring (23.4-30.0) and Alewife (26.9-
304 35.7).

305

Table 6. Comparison of morphometric and meristic characters for Hickory Shad, American Shad, Alewife, and Blueback Herring. Range given for each, if available; usual values reported in literature in parentheses.

Character	Hickory Shad	American Shad	Blueback Herring	Alewife
BD % TL	22.31-26.55	17.2-19.4 ^a	22.1-25.2 ^a	17.8-21.7 ^a
HL % TL	21.34-21.64	22.7-24.0 ^a	18.5-20.6 ^a	20.3-23.7 ^a
EL % HL	18.08-19.10	27.3-32.0 ^a	22.0-26.4 ^a	26.1-32.0 ^a
SNL % HL	25.68-25.71	26.9-32.0 ^a	23.4-30.0 ^a	26.9-35.7 ^a
IOW % HL	16.24-19.28	18.6-21.6 ^a	21.1-26.4 ^a	15.7-21.6 ^a
FLA % TL	11.92-13.43			10.3-12.0 ^a
PVS	14-18	12 ^b -19 ^a	12-16 ^a	12 ^d -17 ^f (14-15) ^a
AVS	17-24	19-25 ^b	18-21 ^d	17-21 (19-20) ^a
SR	49-56	52-64 ^c	46-54 ^d	42 ^d -54 ^g
LSR	15-19	15-16 ^d	13-14 ^e	14 ^d

^a Scott and Crossman 1973, ^b Hill 1956, ^c Walburg and Nichols 1967, ^d Hildebrand 1963

^e Thomson et al 197, ^f Leim and Scott 1966, ^g Miller 1957

306

307 Discussion

308 It is often difficult to discern the causes of morphological and meristic variations between
309 fish populations [22] though it is assumed they might be related to genetic differences or linked
310 to phenotypic plasticity resulting from non-homogeneous environmental factors in each river
311 [19]. However, reasons why there are variations in meristic and morphological characters were
312 not an objective of our study.

313 Instead, our study provides foundational information on the morphometric and meristic
314 variation of Hickory Shad across a large portion of the species range. To complement this study,
315 further research is needed to investigate these characters of Hickory Shad from more southern
316 rivers in Georgia and Florida. This would allow comparison of morphometric and meristic
317 variation across the entire species range and determine if greater geographic distance
318 corresponds to larger variation. It is more likely that adjacent rivers or watersheds share common
319 environmental characteristics compared to rivers separated by large distances, possibly leading to

320 greater variation in morphometrics and meristics. For instance, we were able to obtain 22
321 samples from a small tributary of the Susquehanna, River Maryland at the mouth of Deer Creek
322 (39.613358 N, -76.149024 W), which is near the northern end of the assumed Hickory Shad
323 spawning range. Unfortunately, we were unable to obtain large sample sizes from the
324 southernmost Hickory Shad spawning population of the St. Johns River, Florida, though we did
325 obtain three specimens from the Wekiva River, a tributary of the St. Johns (28.8728226 N, -
326 81.3689402 W). The Wekiva River, Florida, and Deer Creek, Maryland, are separated by
327 roughly 1280 Km.

328 One limitation of this study is that equal sample sizes for each state and watershed could
329 not be collected. Attempts were made to have between 25-50 fish per watershed and a 50:50 sex
330 ratio, but as with most all fisheries work, success in sampling is often not reliable. Multiple
331 factors influenced our ability to collect more samples, including early Hickory Shad spawning
332 runs in some locations, foul weather, low river water levels prohibiting boat access, severe long-
333 term flooding, and expense of traveling to distant locations. It is possible that the morphometric
334 and meristic values presented here for rivers with small samples sizes may not accurately capture
335 the true natural variation of the characters in those populations. Additionally, the timing of
336 specimen collection was not standardized and often started after the spawning run had fully
337 begun, which could have potentially affected this study (i.e., size or sex distributions). Overall,
338 slightly more female specimens (n = 365) were collected than male (n = 330) representing 52.5%
339 and 47.5% of the specimens included in this study, respectively. The difference in the number of
340 males and females could be a product of gear bias and not necessarily representative of the
341 natural populations. For instance, gill nets used to collect some specimens in this study are more
342 selective for larger female Hickory Shad than smaller males. Melvin et al. [19] studying

343 American Shad also found gill nets to be selective for larger females. Furthermore, we
344 experienced a willingness of sport fishers to provide specimens for our study, but reluctance to
345 provide females since most fishers wanted the roe for bait or for personal consumption.

346

347 Sexual Differences

348 Differences observed in the averages of morphometric characters when compared by sex
349 was not a surprising result and is relatively common in fish, though it has never been explicitly
350 described for Hickory Shad. This has significant implications and suggests studies on Hickory
351 Shad must be separated by sex and analyzed in that manner since there is substantial difference
352 between male and female specimens. Melvin et al. [19] came to similar conclusions for
353 morphometric and meristic characters of American Shad and so males and females were
354 analyzed separately.

355

356 Specimen Size

357 It is important to note that the morphometric measurements presented in this study are of
358 frozen and not freshly caught Hickory Shad. It is possible that the freezing and thawing process
359 may slightly alter the shape and or size of some morphometric characters. Melvin et al. [28]
360 reported a significant difference ($P < 0.01$) between length measurements of live American Shad
361 in the field compared to measurements of dead specimens in the laboratory. In the event
362 American Shad were frozen prior to measurement, the length was multiplied by 1.021 to better
363 approximate fresh length [28]. Though fish samples are often frozen by biologists for later
364 processing, future studies should investigate if there is a significant difference between
365 morphometric measurements for fresh versus frozen Hickory Shad and, if so, which

366 measurements are the most robust to the freezing and thawing process. Cronin-Fine et al. [29]
367 found 10 geometric morphometric measurements of Alewife that did not have a significant
368 difference between fresh and frozen specimens. Generally for meristics, the act of freezing and
369 thawing is not problematic since it does not change the counts of meristic features.

370 The freezing and thawing process could also have biased the weight of the fish, but
371 similar to morphometric measurements, the bias is shared across all individuals. Also, gonad
372 weight can be extremely dependent on spawning status (pre or post-spawn), especially for
373 females. Spent females weigh less than ripe and ready-to-spawn individuals, but unfortunately
374 spawning status was not recorded during dissections. There were a few instances of gonads that
375 were unable to be weighed (or sexed) because they were no longer intact or starting to
376 decompose. This was likely a result of freezer storage for an extended length of time, multiple
377 freezing and thawing events, or the length of time from collection till initial freezing. This was
378 not a serious problem; 26 specimens exhibited deterioration and this state was relatively random
379 across rivers. Also, it was likely that some of the individuals not sexed was caused by human
380 error instead of relating to the state of the gonads.

381 The regression equations for relationships between Hickory Shad FL and TL, and
382 between FL and SL, provide a means for converting between the various measurements of fish
383 size. This could be useful for biologists or fishery managers to accurately estimate one length
384 from another in the instance that only one of the measurements was recorded.

385

386 Missing Data

387 Though not a frequent problem in this study, missing data are quite common in
388 morphometric (and meristic) studies [30]. Some of the specimens could not be analyzed for the

389 entire 17 morphometric and four meristic characters due to damage including broken or missing
390 fins, missing scales, and wounds from predation or gear-related injury. Missing scales are not
391 surprising, since the Hickory Shad as well as other clupeids are very susceptible to shedding
392 scales. The frequency of missing values for all characters can be found in Table 5. In our study
393 no imputation procedures (i.e., replacement or regression-based approaches) were used to
394 estimate missing data; instead these values were simply omitted.

395

396 Comparison between Hickory Shad and other Clupeids

397 Most of the morphometric and meristic characters investigated in this study do not serve
398 to easily differentiate Hickory Shad from American Shad, Alewife, or Blueback Herring though
399 careful examination of certain characters can help narrow down the species. One common and
400 definitive way to distinguish Hickory Shad from the other species is by gill raker counts. Though
401 not directly incorporated into this study, a random subset of Hickory Shad specimens was
402 analyzed for gill raker counts. It was determined that Hickory Shad had between 19-22 gill
403 rakers on the lower limb of the first arch (n=463), which is considerably less than the other
404 anadromous *Alosa* species. American Shad typically have 59-76 lower gill rakers on the first
405 arch, Blueback Herring 41-52, and Alewife 38-46, all of which are higher counts [31] due to
406 their diet being different than Hickory Shad, which are more piscivorous [32].

407

408 **Conclusion**

409 Mansueti [7] described Hickory Shad as “The most enigmatic of all estuarine clupeoids”
410 and the intent of our study was to expand the existing taxonomic knowledge of the species.
411 Mitchill [2] used six meristic characters in describing the species: branchiostegal, pectoral,

412 ventral, anal, dorsal, and caudal rays. These six characters were not included in this study
413 because the methods Mitchill used to count them were not available and therefore no direct
414 comparison was possible. Instead, 17 morphometric measurements and four meristic counts not
415 included in the original description of the species were utilized. The information about the
416 anatomical characteristics presented herein are lacking in the literature, though they are well
417 known for most other anadromous fish species. These additional morphological and meristic
418 characters may prove valuable for separating regions or watersheds in future studies. Geometric
419 morphometric analysis may be another viable option to investigate body shape variability. In
420 addition, there still remain many unanswered questions regarding Hickory Shad life history,
421 biology, and stock status that should be addressed so that the species can be properly managed
422 and all spawning populations sustained. Furthermore, the intraspecific variation of Hickory Shad
423 described here could be used to discriminate the different populations using multivariate analysis
424 [33].

425

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435 **Author Contributions**

436

437 **Conceptualization:** Roger A. Rulifson

438 **Data curation:** Roger A. Rulifson

439 **Formal analysis:** Jordan P. Smith; Michael W. Brewer

440 **Funding acquisition:** Roger A. Rulifson.

441 **Investigation:** Jordan P. Smith

442 **Methodology:** Jordan P. Smith, Michael W. Brewer, Roger A. Rulifson

443 **Project administration:** Roger A. Rulifson.

444 **Resources:** Roger A. Rulifson.

445 **Software:** Jordan P. Smith

446 **Supervision:** Roger A. Rulifson, Michael W. Brewer

447 **Visualization:** Jordan P. Smith

448 **Writing - original draft:** Jordan P. Smith

449 **Writing - review & editing:** Roger A. Rulifson, Michael W. Brewer, Jordan P. Smith

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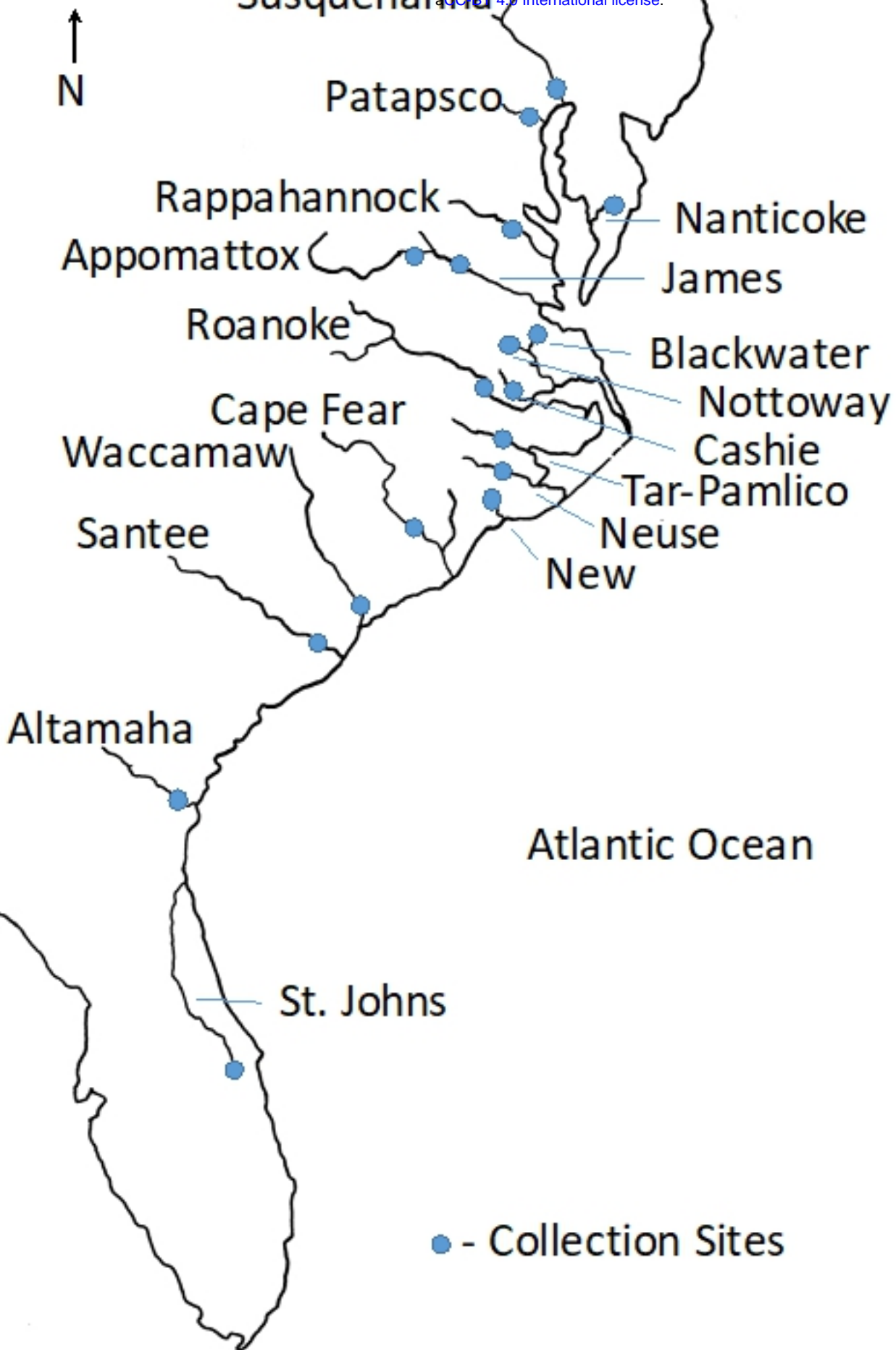
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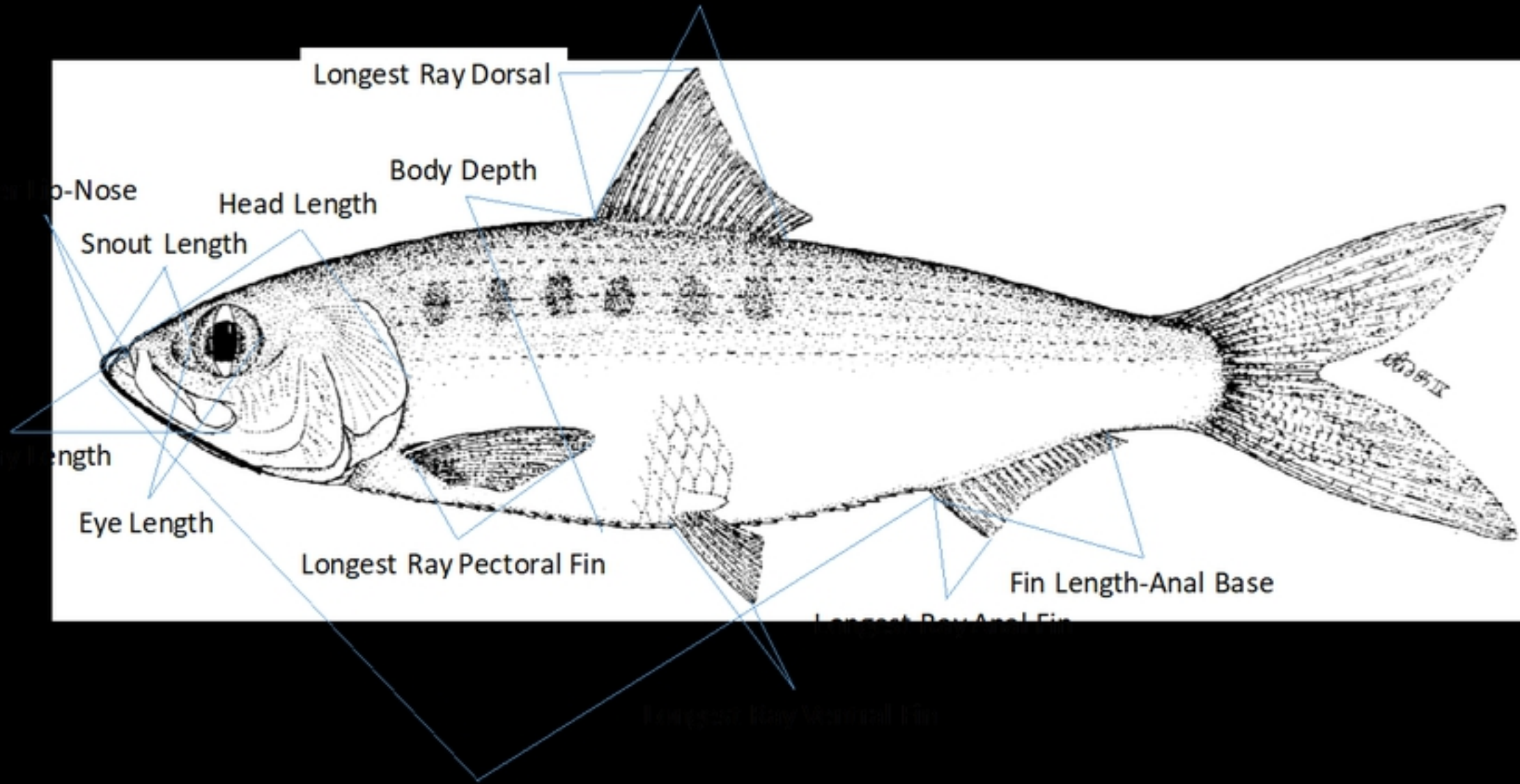
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Figure



Figure