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SYSTEMATICS AND BIOLOGY OF THE GIZZARD SHAD (*DOROSOMA CEPEDIANUM*) AND RELATED FISHES

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ABSTRACT

The gizzard shads, marine and fresh-water herrings of the subfamily Dorosomatinae, are characterized and keys are given to the seven known genera and to the five species of the American genus *Dorosoma (Signalosa* is regarded as a subgenus). The systematics and biology of the eastern gizzard shad, *Dorosoma cepedianum,* are treated in detail. The biological information results largely from a critical survey of papers (unpublished as well as published) dealing with its fecundity, reproduction and development, size, age and growth, abundance, habitat and migration, mortality, parasites and predators, and its food, forage value, and utilization by man. Original drawings of early life-history stages are presented. This summary should enable fishery biologists concerned with inland waters to gain a more comprehensive outlook on the role of the gizzard shad in fish management.

SYSTEMATICS AND BIOLOGY OF THE GIZZARD SHAD *(DOROSOMA CEPEDIANUM)* AND RELATED FISHES

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The herrings of the subfamily Dorosomatinae, known as gizzard and threadfin shads in the New World, comprise seven genera inhabiting Asia, the Indo-Australian region, and North America. Fishery biologists dealing with management of inland waters in eastern North America have been increasingly concerned about the role of the gizzard shad, *Dorosoma cepedianum,* in the ecology of fish populations. Praised in some places as a valuable forage fish, this widespread species has elsewhere so overpopulated lakes that costly and time-consuming control measures have become necessary. A review of the systematics and biology of this species should make possible a more critical assessment of its part in fish management. The present paper is designed to summarize what is known of gizzard shads in general and of *D. cepedianum* in particular.

As a group, the gizzard shads are characterized by the inferior, subterminal or terminal, toothless mouth and the gizzardlike stomach; they were first recognized under the name Chatoëssina by Gunther (1868: 381, 406). The unit was raised to family rank, Dorosomidae, more properly Dorosomatidae, by Gill (1872: 17), and was retained at this level for many years, at least by American ichthyologists. Most workers now refer the group to the Clupeidae and relegate the gizzard shads at most to a subfamily, Dorosomatinae, as did Berg (1940).

The body is generally short and deep (except in the slender young) and moderately to strongly compressed. The scales are thin, cycloid, and more or less adherent; they are absent on the head and may be present or absent on the back between the occiput and the dorsal fin. The abdomen is compressed to a ridge and armed with keeled, bony scutes. The eyes have conspicuous adipose "eyelids." The gill membranes are separate and free from the isthmus; the gill rakers are slender, close set, and exceedingly numerous. There are five to six branchiostegals, and the pseudo-branchiae are large.

Regan (1917: 297) included this subfamily in the Clupeinae because he regarded the separation of the gizzard shads from the other genera centering about *Clupea* as an artificial arrangement. I have not studied the Old World genera and can neither confirm nor dispute Regan's viewpoint. However, since there has been no comprehensive study of the species and genera now referred to the Dorosomatinae, the interrelationships of the Old and New World forms should be regarded as tentative.

As a whole, the gizzard shads are migratory fishes, primarily marine, entering fresh or brackish waters to spawn. Some species, and some populations of single species (such as *Dorosoma cepedianum* and *D. petenense),* are landlocked, completing their life cycle wholly in fresh water. Their food, except early in life, consists chiefly of minute organic particles which are strained by the fine, abundant gill rakers, aided by the accessory pharyngeal pockets (Lagler and Kraatz, 1945; Iwai 1956). The stomach is a short, thick-walled muscular structure like the gizzard of a fowl; the intestine is long and much convoluted, with numerous folds on its inner surface and hundreds of pyloric caeca externally. These digestive specializations further serve to assimilate the minute food of these fishes.

All but two of the seven genera, *Anodontostoma* and *Gonialosa,* are further characterized by having the last dorsal ray prolonged into a conspicuous, elongated filament in the adult. Only *Dorosoma* (including *Signalosa)* inhabits the New World; the other genera are found in Asia and the Indo-Australian region.

In surveying the literature dealing with the

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biology of Dorosoma cepedianum, I have been assisted very materially by the index and references in the library of John van Oosten. Others who have aided in supplying data or references are Reeve M. Bailey, George W. Bennett, S. M. Bower, Gerald P. Cooper, Robert Cummins, Jr., Alfred W. Eipper, Ralph Hile, Melvin T. Huish, Alfred Larsen, Foster D. Roszman, Milton B. Trautman, C. R. Robins, and E. L. Wickliff. I am particularly indebted to Edward N. Warner for allowing me to publish his original drawings (figs. 2-4) and to summarize unpublished material from his doctoral thesis, and likewise to Anthony Bodola for permission to use data from his doctoral dissertation. William L. Brudon made the drawing of the adult (fig. 1).

In the following key, the separation of the Asiatic genera is based on the data given by Regan (1917: 298, 308-317) and on the synopsis presented by Herre and Myers (1931: 234-236).

KEY TO GENERA OF DOROSOMATINAE

1a. Maxillary provided with two supramaxillary bones (the anterior one thinner and more scalelike than the posterior one) - - - - - - - - - - New World *(Dorosoma)*

1b. A single supramaxillary bone - - - - - - - - - - (Old World genera) 2

2a. Last ray of dorsal fin produced into a conspicuous filament - - - - - - - - - - 3

2b. Last ray of dorsal fin not produced into a filament or only weakly so - - - - - - - (*Anodontostoma* and *Gonialosa)* 5

3a. Maxillary flattened, wide posteriorly, without a downward curve at its distal tip; gill rakers of posterior end of ceratohyal nearly as long as longest opposite gill filaments - - - - - - - - - - 4

3b. Maxillary little flattened, very narrow, with a downward angle at its distal tip; gill rakers of posterior part of ceratohyal only half or less than half as long as the opposite gill filaments *Nematalosa* Regan

4a. Dentary normal, not reflected outward, fitting well up inside upper jaw with mouth closed - - - - - - - - - - *Clupanodon* Lacépède.

4b. Dentary anterior to point where it appears from beneath upper jaw (with mouth closed) with its sharp ramus reflected outward, its edge opposed to edge of upper jaw - - - - - - - - - *Konosirus* Jordan and Snyder

5a. Maxillary straight, thin, transversely expanded, tapering distally. Last dorsal ray little if at all produced - - - - - - - - - - *Anodontostoma* Bleeker

5b. Maxillary slender, distally slightly expanded and curved downwards. Last dorsal ray not produced. - - - - - - - - - - *Gonialosa* Regan

Genus *Dorosoma* Rafinesque

Gizzard shads, threadfin shad

Dorosoma Raflnesque, Western Rev. and Misc. Mag., 1820: 2 (3) : 171 *(see* Fowler 1945: 6, 8) ; Ichthyologia Ohiensis, 1820: 39. Type species by monotypy, *D. notata* = *D. cepedianum* (LeSueur) . Type locality: Below the falls of the Ohio River.

Signalosa Evermann and Kendall, 1898, Bull. U.S. Fish Commission, 17 (1897) : 127. Type species, *Signalosa atchafalayae* = *D. petenense* (Gunther). Type locality: Atchafalaya River, Melville, La.

Common name.—The fishes of this genus have generally been referred to as gizzard shads because of the gizzardlike muscular stomach. The vernaculars, skipjack, hickory shad, mud shad, sawbelly, jack shad, et cetera, were formerly applied to D. cepedianum and are still used locally; the name aucun is used in Quebec. Threadfin shad has been adopted as the vernacular for D. petenense.

Generic characters.—Clupeid fishes with the last ray of the dorsal fin prolonged into a slender filament (absent or inconspicuous in the young), thus resembling their marine New World relative Opisthonema. The mouth is small to moderate, terminal, subterminal, or inferior, the lower jaw included or the jaws subequal. Mouth toothless in adult, but young with a row of fine teeth on upper jaw. Maxillary with two supramaxillary bones. Snout short and rounded. Stomach gizzardlike, the intestine long and much convoluted, with numerous pyloric caeca. Body compressed, silvery, the abdomen armed with bony scutes (total, 23-32). Dorsal rays 9-15; anal rays 17-38; pectoral rays 12-17, pelvic rays 8; caudal rays 19 (17 branched), rarely 17 or 18. Scales cycloid, thin, 40-83 along side. Vertebrae (including urostyle) 40-51.

Range.—All the species except D. smithi are confined to the Atlantic drainage of North and

Middle America (Canada to Nicaragua). They are found from the Great Lakes–St. Lawrence River basins, southern South Dakota, Nebraska, and Minnesota, and from about latitude 40° N. on the Atlantic seaboard of New Jersey and southeastern Pennsylvania southward to Lake Nicaragua (but with discontinuous distribution from northern Guatemala and British Honduras to Nicaragua). *D. smithi* is known only from coastal streams of northwestern Mexico, in Sonora, Sinaloa, and Nayarit.[1]

Species.—Five species of *Dorosoma* are recognized, four in the subgenus *Dorosoma* and one, *D. petenense,* in the subgenus *Signalosa.* They may be distinguished by means of the following key. The resemblances between *Dorosoma* and *Signalosa* are numerous, the differences few, with no sharp structural gaps. The form and position of the mouth afford the most reliable means of distinction. The relationships of the five species seem to be better expressed by referring them all to *Dorosoma,* using subgenera to indicate the lesser phyletic lines.

[1] The record for Nayarit is based on 123 specimens in the University of Michigan Museum of Zoology (UMMZ 171979) collected in 1955.

KEY TO SPECIES OF DOROSOMA

1a. Mouth terminal, ventral edge of upper jaw smooth. Fewer than 50 scales in lateral series, regularly arranged. Anal rays 17-27, usually 20-25. Vertebrae 40-45. Atlantic slope from Florida, Tennessee, and Oklahoma west and south to northern Guatemala and British Honduras ------ Subgenus *Signalosa, D. petenense* (Gunther)

1b. Mouth subterminal or inferior, ventral edge of upper jaw with slight to pronounced notch (except in young). More than 50 scales in lateral series, irregularly arranged. Anal rays 22-38, usually 29-35 (where range overlaps that of *Signalosa).* Vertebrae 43-51 (47-51 where the two subgenera coexist) ------------- Subgenus *Dorosoma*

2a. Lateral scales 52-70, usually 58-65; scales around body 36-45; vertebrae 48-51. Atlantic drainage of eastern North America south to Rio Penuco, Mexico --------------------------- *D cepedianum* (LeSueur)

2b. Lateral scales 70-83, usually 73-78; scales around body 46-60; vertebrae 43-48 3

3a. Dorsal filament long, its length as measured from dorsal origin 0.95 to 1.4 times, usually 1.1 to 1.3, in distance from pelvic insertion to tip of snout; anal base 1.1-1.4 in same distance; anal rays 29-38, usually 32-35. Atlantic slope of Mexico and northern Guatemala (Rio Papaloapan to Rio Usumacinta) -- *D. anale* Meek

3b. Dorsal filament short, its length as measured from dorsal origin 1.4-1.85, usually 1.5-1.8, in distance from pelvic insertion to tip of snout; anal base 1.6-2.2 in same distance; anal rays 22-31, usually 23-29 ---- 4

4a. Mandible long, nearly one-half length of head; scales around caudal peduncle 20-26; dorsal rays usually 13 (12-14). Lakes Managua and Nicaragua, Nicaragua -------------- *D. chavesi* Meek

4b. Mandible short, less than one-third length of head; scales around caudal peduncle 28-31; dorsal rays usually 11-12 (9-13, rarely 9, 10, or 13). Pacific slope of northwestern Mexico (Sonora to Nayarit) -- *D. smithi* Hubbs and Miller

In this work, only *Dorosoma cepedianum* is treated in detail. Information on the systematic characters, growth, and relationships of the other three species of the subgenus *Dorosoma* appeared elsewhere (Miller 1950). Recent interest in the threadfin shad, *Dorosoma (Signalosa) petenense,* as a forage fish has resulted in the experimental planting of this species in various States (Parsons and Kimsey, 1954; Kimsey 1954). Relatively little published data is available on the systematics and biology of the threadfin shad.

Dorosoma cepedianum (LeSueur)

Eastern gizzard shad, hickory shad, skipjack, mud shad

(Figures 1-4)

Synonymy.—In the following partial synonymy, only the references to original descriptions of the forms now regarded to be conspecific with *Dorosoma cepedianum* are given.

Megalops cepediana LeSueur, 1818, Jour. Acad. Nat. Sci. Phila., 1: 361-363 (original description ; markets of Baltimore and Philadelphia, hence usually given as Chesapeake and Delaware Bays).

Clupea heterura Rafinesque, 1818, Amer. Month. Mag., 1818: 354 (original description ; Ohio River).

Dorosoma notata Rafinesque, 1820, Western Rev. and Misc. Mag., 2: 172 (original description ; falls of the Ohio River).

Chatoëssus ellipticus Kirtland, 1838, Rept. Zool. Ohio, in Second Ann. Rept. Geol. Surv. Ohio, Columbus, 1838: 169, 195 *(nomen nudum,* Ohio; same as *Dorosoma notata).* 1844, Boston Jour. Nat. Hist., 4 (2) : 235-237, pl. 10, fig. 1 (original description, comparisons, occurrence in Ohio, habits, mortality ; Ohio River and its tributaries).

Chatoëssus insociabilis Abbott, 1861, Proc. Acad. Nat. Sci. Phila., 12 (1860) : 365-366 (original description, habits ; "sturgeon pond" 2 miles below Trenton, N.J.).

Megalops bimaculata L[illegible] S[illegible], 1848, in C[illegible] and Valenciennes, H[illegible]. Nat. P[illegible]., 21: 104 (*nomen nudum;* [illegible] with *Chatoessus oepedianu8* by Valenciennes).

Dorosoma cepedianum exile Jordan and Gilbert, 1883, Proc. U.S. Natl. M[illegible]., 5 (1882): 585 (original description, based on 2 specimens, from Galveston, Tex.).

Diagno8i8.—A gizzard shad with 52-70 lateral scales? 36-45 scales around the body, 48-51 (usually 50) vertebrae, 25-36 anal rays, and preponderantly 18 + 12 ventral scutes.

The dorsal filament is comparatively long. As in the other species of *Dorosoma*, its length varies greatly with age, and statements regarding this structure have little meaning unless accompanied by data on the size of the specimen. The filament is inconspicuous or absent in young fish, increasing in length with age up to a certain size range (around 200 mm.?), and then decreasing in relative size.

Deseription.—Body depth 2.3-3.1 in standard length (all measurements "stepped off" with a pair of precision dividers); predorsal length 1.85-2.05; prepelvic length 2.0-2.35; anal origin to caudal base 2.4-2.8; head length 3.0-3.9; length of dorsal filament 3.1-6.5 (0.8-2.0 in head length); length of anal base 3.2-3.9 (0.75-1.25 in head length). Head width 1.8-2.5 in head length; eye length 3.3-5.4; snout length 5.0-6.0; bony width of interorbital 3.3-4.5; length of upper jaw 3.5-4.2; length of mandible 2.6-3.3; length of caudal peduncle 2.4-3.5; depth of caudal peduncle 2.45-3.4; length of pectoral 1.15-1.45; length of pelvic 2.0-2.5; length of dorsal base 1.85-2.6; length of lower lobe of caudal 0.7-1.1, typically longer than anal base (rarely subequal).

Dorsal rays 10-13, average 11.61 in 197 specimens; anal rays 25-36, 31.32, in 195; pectoral rays 14-17, 15.52, in 288 (144 individuals); pelvic rays 8, rarely 7; and caudal rays 19. Lateral scales (first scale counted was first one lying above uppermost corner of gill opening) 52-70, 61.06, in 67; scales between dorsal and anal fins 19-24, 21.77, in 52; scales around body (beginning with first scale just in front of left pelvic fin) 36-45, 41.03, in 73; and scales around caudal peduncle (slenderest part) 16-20, 18.02, in 53. Prepelvic scutes 17-20, 17.99, in 196; postpelvic scutes 10-14, 11.76, in 197; total ventral scutes 27-32, 29.74, in 196. Number of vertebrae (including urostyle) 48-51, 49.83, in 42 specimens. Gill rakers very numerous and fine, those on first arch number about 90 to 300 at standard lengths of

[2] For method of counting scales see Miller (1950: 388-389).

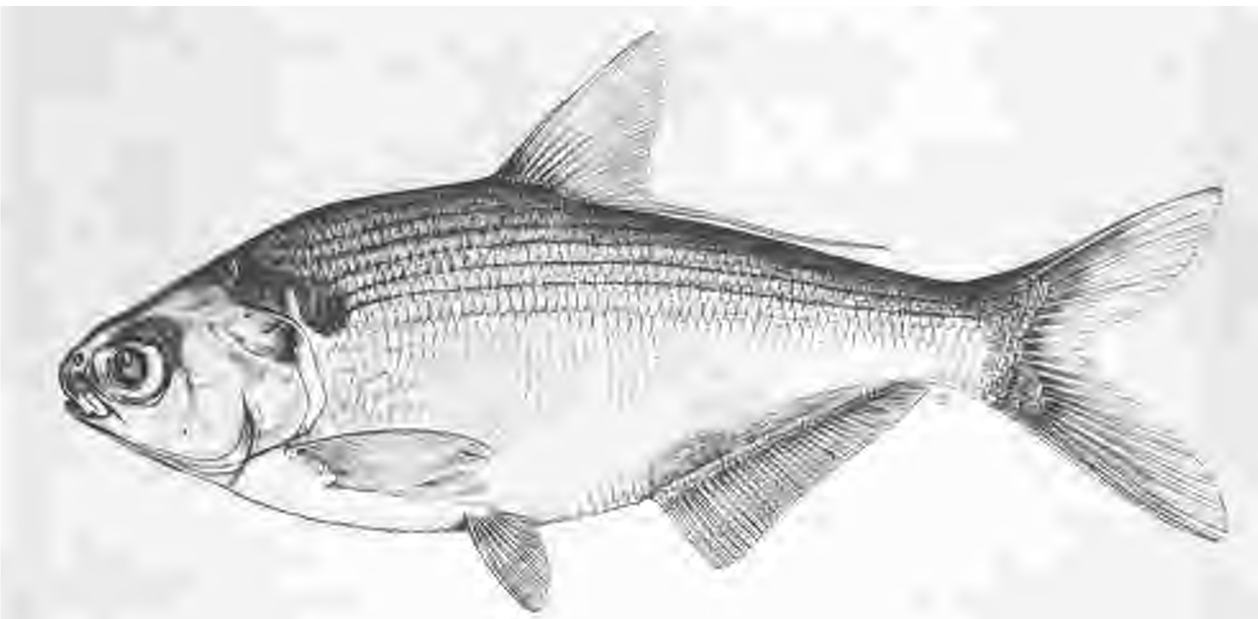

FIGURE 1.—A[illegible] female *Doro8oma cepedianum* (UMMZ 128171), 180 [illegible]. standard length (about 9 inches total length), from Lafayette County, Arkansas. (Drawn by W. L. B[illegible].)

20-65 mm., about 350 at 95 mm., and 412 in a specimen 157 mm. long.

Although the adult (fig. 1) is a deep-bodied, strongly compressed fish, the young (fig. 4, c) is slender, minnowlike, and nearly cylindrical. The maxillaries on young specimens have a few minute teeth on the lower edge which are lost with age. The highly specialized digestive tract of the adult is also lacking in the young, which have an almost straight intestine and no pyloric caeca. By the end of the first summer, however, the young possess the specializations of the adult.

No external characteristics will reliably distinguish the sexes.

Color.—In life the body is silvery bluish over the back and upper sides but milky white on the abdomen, and often has brassy or golden reflections from the scales. There are six to eight horizontal, dark stripes along the upper sides above the level of the middle of the shoulder spot, extending from behind the head to the base of the caudal fin. The large, round dark spot behind the opercle, so prominent in the young and half-grown, is lustrous purple. In adults, the dorsal fin is nearly uniformly dusky; the caudal fin is dusky but darkened on its outer third; the outer two-thirds of the anal fin is dark, the basal third lighter, with melanophores sprinkled over most of the fin; the pectorals and pelvics have their outer halves darkened, paling basally. The top of the head, snout, upper jaw, and upper part of the opercle are pigmented in young and adult; the rest of the head is silvery. In young-of-the-year (up to about 4.5 inches, total length), the dorsal fin is sparsely but uniformly sprinkled with chromatophores; the caudal fin is similar but has more pigment cells; the anal, pectoral, and pelvic fins are almost unpigmented. A good color plate of the species is given by Forbes and Richardson (1920, opposite p. 46).

Variation.—Insufficient data concerning certain variations in this species led to the recognition of at least three nominal subspecies; namely, D. *c. cepedianum* (LeSueur), on the Atlantic slope southward and westward along the Gulf of Mexico; D. c. heterurum (Rafinesque), in the middle and upper parts of the Mississippi River system and the Great Lakes-St. Lawrence watershed; and D. c. exile Jordan and Gilbert, in coastal streams from Texas to northeastern Mexico. As Jordan (1882: 871) stated, "The difference between *heterurum* and *cepedianum* is not great, the greater arch of the back in cepedianum being the main difference." It was soon recognized that this minor feature does not characterize these inland populations of gizzard shad. The form described from Texas (Galveston) has persisted much longer in the literature (e.g., Fowler 1945: 22, 366). This nominal subspecies, very briefly and inadequately described, was based solely on the supposedly slenderer body (body depth about 2.9-3.3, rather than 2.5-2.7 in specimens from Indiana and South Carolina), whence the Latin word exile, meaning slender. Unfortunately, the two type specimens (USNM No. 30913) have not been found. Although I have not examined specimens from Galveston, the ratios of body depth to standard length (table 1) demonstrate that subspecies of Dorosoma cepedianum cannot be recognized on this basis.

TABLE 1.—*Variation* in body depth in regional samples of Dorosoma cepedianum

Area	Range in standard length (mm.)	Ratio	Average	Number of specimens
Maryland to North Carolina	61-211	2.3-2.95	2.65	26
Middle and upper Mississippi R.-Great Lakes systems	78-215	2.35-2.85	2.62	36
Western Florida to Louisiana	84-204	2.5-3.1	2.69	20
Texas	56-196	2.45-2.9	2.69	29
Northeastern Mexico	81-227	2.4-2.9	2.68	12

NOTE.—The depth was stepped into the standard length by using fine dividers under magnification.

The dark shoulder spot (fig. 1) is said to disappear with age but is variably developed in different populations. This spot, present in young and half-grown, is typically seen in small adults and frequently in large ones. For example, the nominal species Chatoessus insociabilis Abbott was based in part on the retention of this marking in large adults. This spot was well developed in a freshly preserved series of adults, 165 to 204 mm. in standard length, from the Escambia River, Florida.

Study material.—The proportions used in the description are based on 74 specimens, between 78 and 247 mm. standard length, representing localities in Florida, Alabama, Mississippi, Louisiana, Texas, and northeastern Mexico, and from Oklahoma, Arkansas, Tennessee, Missouri, Kansas, Nebraska, Iowa, Illinois, Indiana, Ohio, and Michigan. Specimens from Atlantic coastal waters

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are not represented in the general description, but they were used in a study of variation in body depth. Counts of fin rays, scales, and ventral scutes are based on 51 to 200 specimens distributed from Michigan and Maryland southward and westward to Tamaulipas, San Luis Potosí, and Querétaro, Mexico. Vertebral counts are based on 42 specimens from localities scattered over the range of the species.

Reproduction and development.—Spawning takes place in fresh water (Gunter 1938: 71) from late winter (mid-March) through most of the summer (at least to August 20) in sloughs, ponds, lakes, and large rivers. A group of males and females swimming near the surface begin to roll and tumble about each other in a mass, the eggs and sperm being ejected during this activity. The sticky eggs slowly sink to the bottom or drift with the current, readily becoming attached to any object they may contact. At times the small eggs cover aquatic vegetation, particularly streamers of green algae adhering to rocks, forcing the plants to the bottom of the pond or river. Gizzard shad generally spawn on a rising temperature although on one occasion Trautman (personal communication) found them spawning on a falling temperature at Buckeye Lake, Ohio. Langlois (1954: 224) observed gizzard shad spawning along shore, at a depth of 6 to 12 inches, on May 29, 1935, in North Reservoir, Akron, Ohio; when oviposition occurred (67° F.) a female was flanked on each side by a male.

The bulk of the populations that inhabit the warm to temperate waters of the United States (28° to 41° N. Lat.), spawns during April, May, and June at temperatures between about 50° and 70° F., the onset of spawning varying with the season. For example, in experimental ponds at Auburn, Ala., gizzard shad hatched at the end of April in 1941 but first appeared in the middle of March in 1942; in 1941 the last brood hatched on August 20 but in 1942 hatching continued only into July (Swingle 1949: 53). In Chickamauga Reservoir on the Tennessee River, a few miles above Chattanooga, Tenn., most individuals had spawned by the last week of May in 1942; all adults examined on June 9-10 had spawned, about two-thirds of the females studied June 1-5 were spent, and very few adults had spawned prior to May 22 (Eschmeyer, Stroud, and Jones, 1944: 96). In Norris Reservoir, Tenn., shad spawned in 1943 between May 18 and June 8, when surface temperatures varied from 73.5° to 81.7° F.; in 1944 most of the spawning took place between May 15 and June 1, with the temperature from 78° to 84° F. (Dendy 1946b: 121). Gonads were ripening near the end of January 1954 in Lake Panasoffkee, Fla., with the bulk of spawning taking place in March and April and completed in May (Moody 1957: 30, 38). Near the northern limit of its range, in Fort Randall Reservoir, S. Dak., all adults caught after July 6, 1955, had spawned and most of those obtained before June 24 were green, indicating a short and comparatively late spawning period (Shields 1956: 30). Bodola[3] found that water temperature during development of the eggs is probably more influential in determining the time of peak spawning than is the water temperature immediately preceding the spawning period.

At Buckeye Lake, Ohio, a shallow impoundment in the Ohio canal system, the gizzard shad begins to spawn when the water warms to 60° F., usually during the first part of May but varying from year to year. The spawning period normally extends over about 2 weeks, with an occasional ripe female found later in the season (one was taken in the latter part of July) (Warner 1941: 639; observations made 1938-40).

In Iowa, the species is reported to spawn in late April or early May (Harlan and Speaker, 1956: 60). In the vicinity of Greenwood, Miss., a gravid female was taken in June 1925 (Hildebrand and Towers, 1928: 114). In Chesapeake Bay, Md., the gizzard shad spawns in "early summer" (Hildebrand and Schroeder, 1928: 107). Ripe males and females were recorded from the central part of the Illinois River, Ill., during May (Forbes and Richardson, 1920: 47). A spring spawning migration (dates not given) up the Mississippi River is reported by Gowanloch (1933: 215).

The embryology and early life history of the gizzard shad have been studied by Edward N. Warner, and reported in abstract (Warner 1941). Dr. Warner has kindly permitted me to use material from his doctoral thesis that did not appear in the abstract, including drawings of the embryonic and larval stages (figs. 2-4).

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[3] Bodola, Anthony, The life history of the gizzard shad, *Dorosoma cepedianum* (LeSueur), in western Lake Erie. Ph.D. thesis, Ohio State University, 1955: i-xi, 1-130, figs. 1-44.

The nearly transparent, fertilized egg measures about 0.75 mm. in diameter after fixation. When first extruded, it is irregular and wrinkled but soon becomes spherical in the water; it is creamy yellow as seen under the microscope. There is no perivitelline space between the enclosing capsule and the *egg,* which is not free to turn. There is a heavy adhesive layer around the outside pierced by a micropyle. The newly laid egg sticks to any object it contacts. The yolk consists of closely packed, slightly granular globules, and there is one large clear oil globule and one or two (rarely 3 to 5) smaller ones.

Shortly after fertilization (15-20 minutes at 80° F.), the cytoplasm becomes raised at one side of the yolk to form a single blastomere. After about an hour of incubation (80° F.), the first cleavage furrow is complete, bisecting the blastomere. During the early cleavage stages and later, the egg of this species follows a course that is typical of teleostean development.

The embryo (fig. 2, *a* to *f;* fig. 3, a and b) hatches after 95 hours of incubation at 62° F. (or about 36 hours at 80° F.), and a continuous fin is formed around the posterior two-thirds of the body (fig. 3, c) . Bodola *(we* footnote 3) found the hatching time varied from about 36 hours to approximately 1 week, depending on water temperature. The prolarva (fig. 3, c-e) immediately sinks toward the bottom, head downward. After sinking a few inches, swimming movements orient the head region upward and the prolarva continues to swim upward for about the same distance that it sank. Such alternate sinking and rising movements characterize the behavior of the gizzard shad for the first 2 days after hatching. The average total length of the prolarva is 3.25 mm., its body depth (including finfold) 0.2 mm.; the length of the yolk sac is 0.8 mm. There are fribout 32 pairs of somites. At this stage the small fish is so transparent that it is seen only with difficulty in a jar of water. The unpigmented eyes are fairly well-developed and possess a lens, but a wide choroid fissure persists. The conspicuous auditory pits lie a short distance back of and slightly above the eyes. The head is flexed downward at an angle of 90° and is joined to the anterior margin of the yolk sac. The hind gut lies outside of the body wall proper and

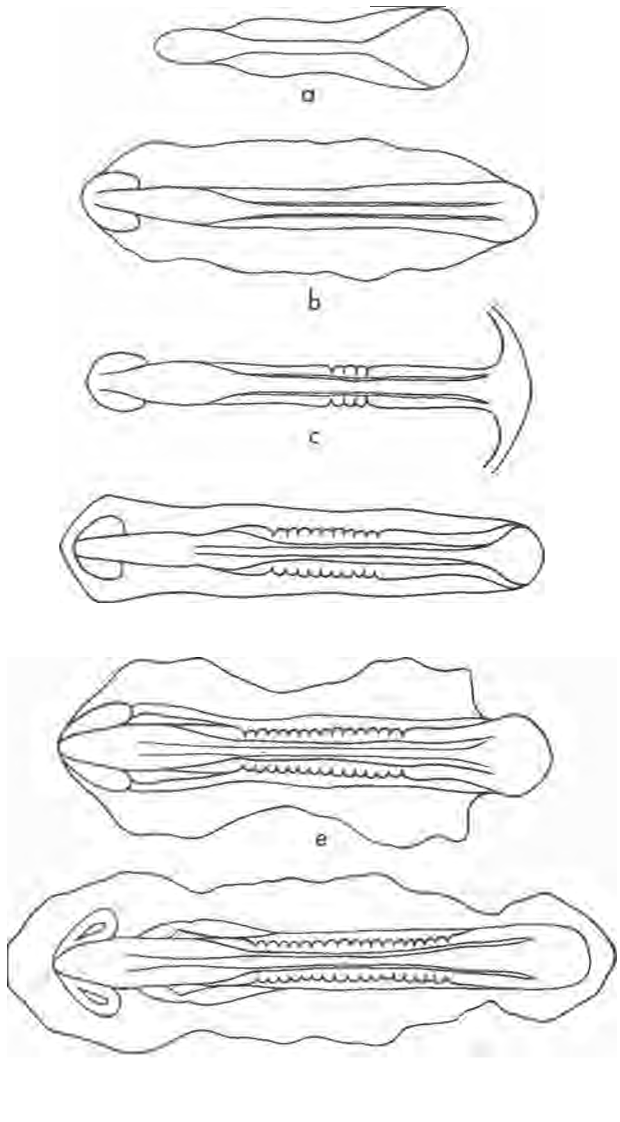

FIGURE 2.—Embryonic development of gizzard shad at various stages after fertilization at a water temperature of 62° F. a, Early embryo, 27 hours ; b, embryo of 2 somites, 33 hours ; c, embryo of 3 somites, 38 hours ; d, embryo of 9 somites, 43 hours ; e, embryo of 14 somites, 48 hours ; f, embryo of 17 somites, 52 hours.

extends posteriorly to the level of the last somite, where it turns downward and ends in the vent at the margin of the finfold.

The 1-day-old prolarva (fig. 3, d) averages about 5.5 mm. total length. The head has lost its distinct downward flexure, and the heart is now pulsating although there is no pigmented blood. The oral plate on the ventral surface of the head is perforated but the pharynx is not open

[1] I follow the terminology recommended by Hubbs (1944).

into the mouth cavity. The choroid fissure of the eye is closed, and the anlagen of the pectoral fins are evident in the form of small rounded buds. There is still no pigmentation, most of the yolk sac is absorbed, and there are about 40 myotomes.

The 3-day-old prolarva (fig. 3, *e)* is about 6.5 mm. long. The cartilage of the lower jaw is now forming and there are four gill arches but no gill filaments. The pectorals are small, paddle-like appendages and only a vestige of the yolk sac remains. The alimentary canal appears to be complete. There is a row of conspicuous chromatophores on each side of the body along the roof of the alimentary canal dorsal to the yolk sac. A row of pigment cells also occurs along the base of the finfold, from the yolk sac to the vent. The vent is close to the body, in a notch at the base of the finfold.

Subsequent stages (postlarval, fig. 4, *a-c)* were obtained from Buckeye Lake, hence their ages are unknown. Development beyond the 3-day stage consists primarily of growth in length and depth and the gradual acquisition of adult characteristics. The dorsal, caudal, pectoral, pelvic, and anal fins develop in the sequence named. The internal folds of the intestine develop (seen in a 10.8-mm specimen, fig. 4, a) and the operculum

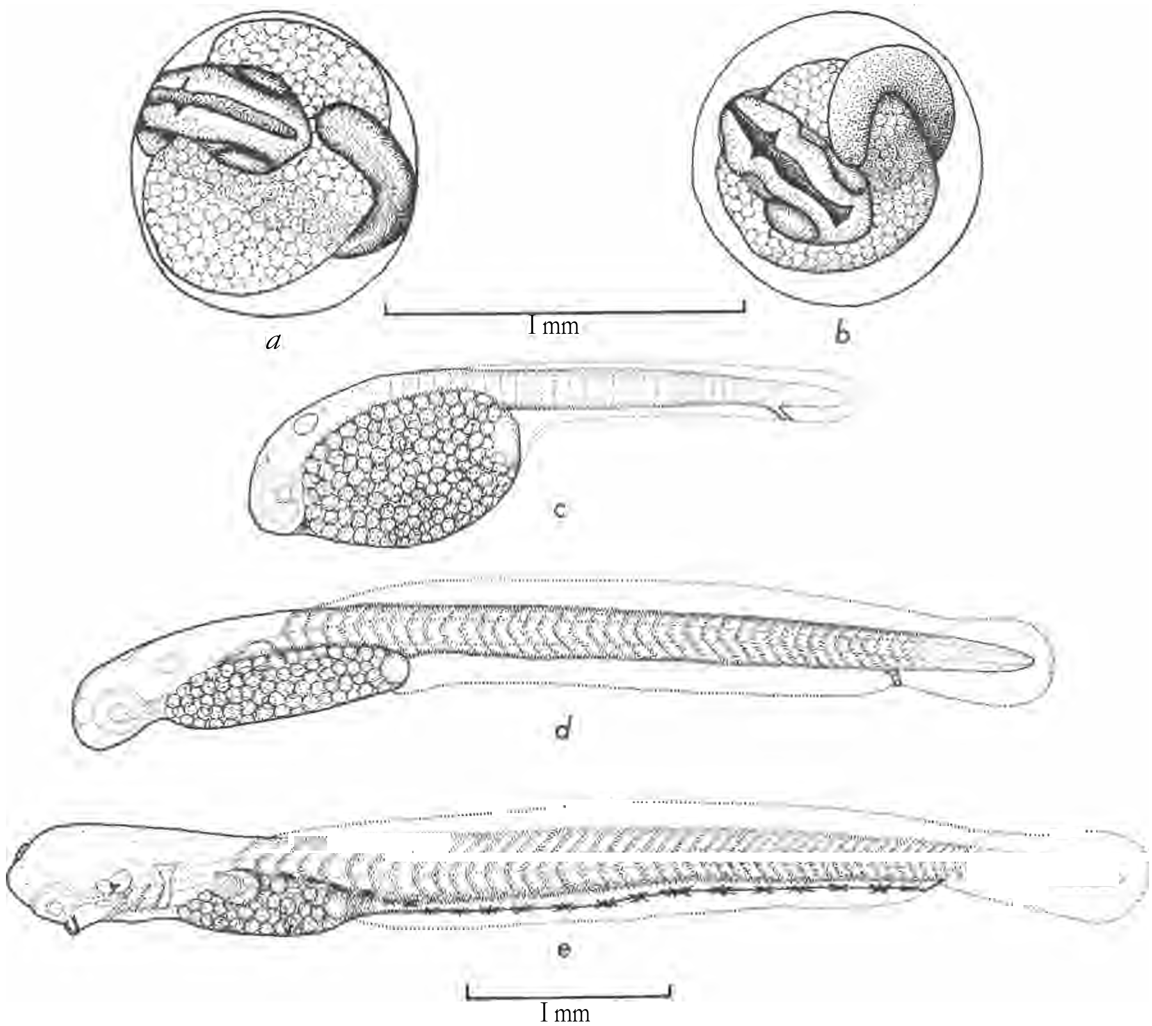

FIGURE 3.—Embryonic and larval development of gizzard shad at various stages after fertilization at a water temperature of 62° F. a, Complete circle of yolk, 60 hours; *b,* advanced embryo, 70 hours ; *c,* hatching stage, 32 somites, 95 hours ; 4, 1-day-old larva in finfold stage, 119 hours; e, 3-day-old larva in primary pigmentation stage, 162 hours.

grows posteriorly to cover the gills. The auditory pit becomes invisible from the surface by the overgrowth of the head skeleton and musculature. The pigmentation becomes more prominent, especially along the dorsal surface and on the dorsal and caudal fins. Bodola (see footnote 3) was unable to rear the young beyond the 10th day after hatching, at which time his fry were slightly more than 6 mm. long.

The larvae of the gizzard shad may be distinguished from those of fishes with which they may be confused by the long gut (1.5 to 2.0 times the total length of the fish), the retarded development of the single dorsal fin, and the elongated anal fin (22 rudimentary rays at 17.5 mm., 30 to 34 at 10 to 22 mm. total length).

Fecundity.—In his study of the gizzard shad in Lake Erie, Bodola (see footnote 3) found considerable variation in the estimated number of eggs per individual female. Two females of age-group I, averaging 231 mm. in standard length, had an average of 59,480 eggs; 5 females of age-group II, 291 mm. long, averaged 378,990 eggs; 3 individuals of age-group III, averaging 331 mm. long, had 344,780 eggs; 2 in age-group IV, 356 mm., averaged 308,750; and 1 female of age-group VI, 355 mm. long, had an estimated 215,330 eggs. Although meager, the data show that precocious shad have few eggs, that the II-group individuals have the most eggs, and that egg production declines with successively older groups. Fish weighing between 500 and 600 grams

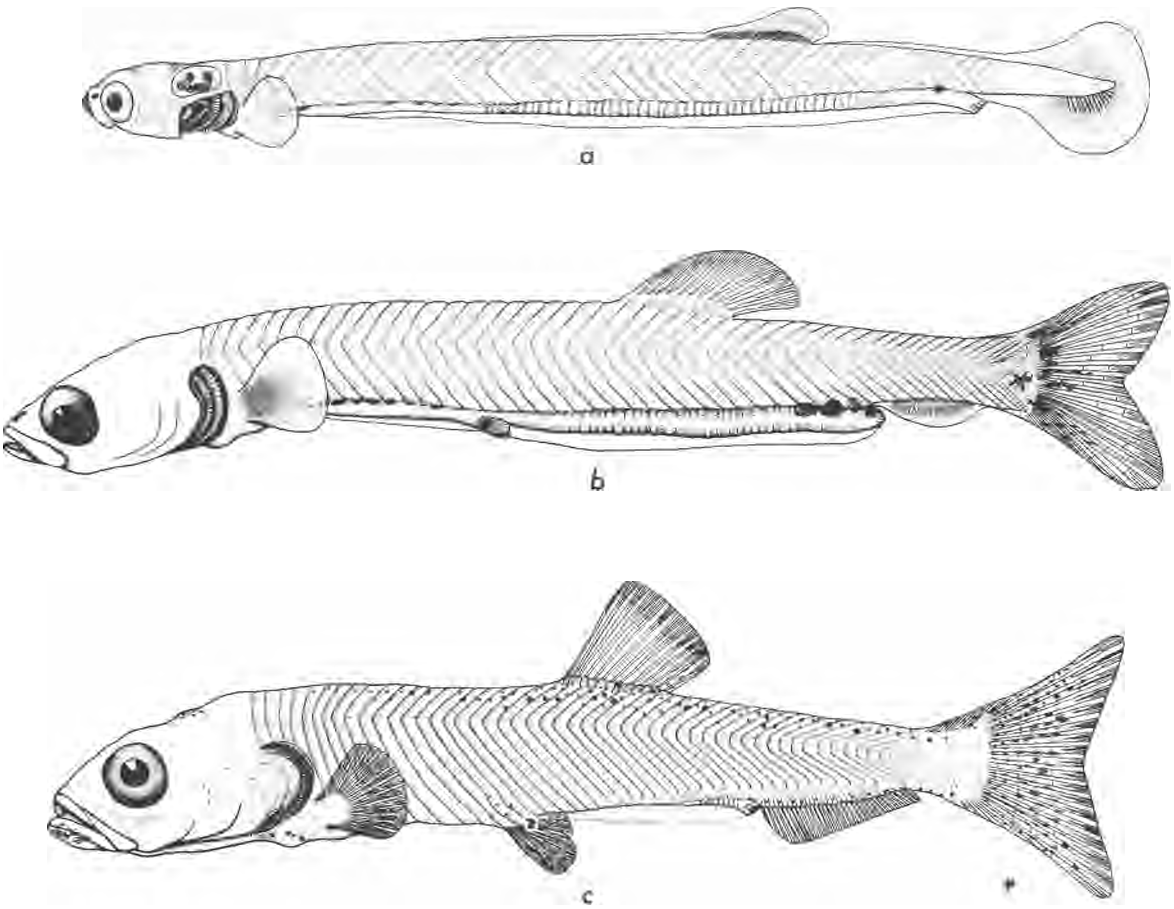

FIGURE 4.—Larval development of gizzard shad collected in plankton net, Buckeye Lake, Ohio. a, Eye-pigment stage, length 10.8 mm., age unknown ; b, pelvic-fin stage, 17.5 mm., age unknown; c, definitive-fin stage, 22.0 mm., age unknown.

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produce the most eggs. A ripe female 315 mm. long, taken in June 1925, near Greenwood, Miss., contained approximately 50,000 eggs according to Hildebrand and Towers (1928: 114).

Age and *growth*.—Data on the age and growth of the gizzard shad have been summarized recently by Carlander (1950: 24-25; 1953: 282-283) and further treated by subsequent authors. The following summary is taken in large part from the original papers cited therein.

In Foots Pond, Ind., growth of young-of-the-year, as noted in samples taken on four successive dates in 1940, was as follows (standard length range, in mm., followed by average length): 19.0-44.5, 31.4 (71 specimens, June 26); 32.0-65.0, 57.0 (29, July 10); 45.0-79.0, 66.6 (42, August 20); and 61.0-88.0, 72.4 (70, November 13). Growth is very rapid in the first 5 to 6 weeks of life and gradually tapers off as the season progresses (Lagler and Applegate, 1943: 104-105). At the end of the first summer, an average total length of about 4 inches is attained (Indiana and Ohio); total length is about 4.5 inches in the Chesapeake Bay region, and 5.0 inches in Tennessee and Oklahoma.

A summary of the age and growth of Dorosoma in Foots Pond and Grassy Pond, Ind., as determined from samples collected between June 26 and August 28, 1940, is given in table 2. Studies on gizzard shad from the Chickamauga Reservoir, Tenn., in 1942, showed that 1-year-old fish had a modal length of 7 inches in June and about 7.5 inches by fall; 2-year-old fish were about 8.5 inches long in April; and the largest shad were about 16 inches long. Young shad (born in late May or early June) showed an average length of approximately 1.5 inches by the last week in June, 2.5 inches by mid-August, and 3.5 inches by late September (table 3). A summary of growth in Grand Lake, Okla., over a 13-year period (Jenkins 1953a: 53), showed that here, as at Herrington Lake, Ky., first-year growth is only about 4.5 (rather than 7) inches, thus extending the time during which gizzard shad are available as a forage fish. The average length of gizzard shad in Crab Orchard Lake, an artificial impoundment in southern Illinois, was only 4.0 inches at the end of the first year, 5.4 inches at the second year, and 6.6 inches at the end of the third year (Lewis 1953).

TABLE 2.-Age of gizzard shad and average lengths of fish in each age group in two Indiana ponds, June 26-August 28, 1940

[From Lagler and Applegate, 1943: table 3]

Item	Age group					
			II	III	IV	
Number of specimens	242	38	84	81	25	6
Size range (mm.)	19-79	130-180	172-222	180-238	199-250	230-309
Size range (in.)		7-9	9-11	9-12	10-13	11-15
Average standard length (mm.)	41	152	193	207	223	256
Average total length (in.)		7.6	9.7	10. 5	11.3	12.8

[1] Based on number of annuli.

TABLE 3.-*Length* distribution of *11,240* young-of-the-year gizzard shad in Chickamauga Reservoir, Tenn., *1942*

[From Eschmeyer, Stroud, and Jones, 1944: table 14]

Total length (mm.)	June 24-30 [1]	July 6-21	August 3-20	September 2	September 28-29	October 27
21-26	123	7	---------			
27-32	202	26	---------			
33-38	366	509	1	---------		
39-44	546	767	10	---------		
45-50	336	269	58	---------		
51-56	221	213	126	11		
57-62	207	187	154	31	22	1
63-68	123	115	157	183	62	3
69-74	74	122	165	464	56	22
75-80	27	166	135	478	97	92
81-86	7	105	129	336	81	224
87-92		44	77	161	04	362
93-98	1	11	59	112	37	214
99-104		3	26	53	18	76
105-110		2	13	11	32	31
111-116			2	4	11	18
117-122			1	---------	4	7
123-128				2	2	4
129-				1		1
Total	2,233	2,546	1,113	1,847	2,446	1,055

[1] Five samples collected on June 16, 24 (3 samples), and 30.
Four of the six samples taken were collected on July 7.
[3] Four collections made on August 3, 12, 19, and 20.

At the end of the first year of life in Fort Randall Reservoir, S. Dak., the average total length of the 1954 age group was 5.1 inches (170 specimens) and of the 1953 age group 7.0 inches (Shields 1956: 30). Somewhat greater average lengths are given for samples from Black River, Mo., by Patriarche and Lowry (1953: 99-105).

The gizzard shad typically matures in its second or third year and lives for at least 7 years, in Oklahoma (Jenkins 1953a: 54) and Lake Erie (Bodola; see footnote 3, p. 376). Patriarche (1953: 249) found 10-year-old gizzard shad in Lake Wappapello, Mo., but stated that in other Missouri reservoirs the species lives no longer than 5 or 6 years. Gizzard shad in Lake Newnan, Fla., average about 10 inches (total length) at the end of their first year of life, about 12.5 inches at the end of the second year, and about 13.6 inches at the completion of the third year—thus indicating rapid growth coupled with a very short life span. Only about 5 percent approach their third actual year of life and none over 4 years old was found (Berry 1958).

From 70 to 80 percent of the annual growth of gizzard shad in Lake Erie takes place during June, July, and August or July, August, and September, depending on the season and the age of the fish. The species grows little if at all during winter, when considerable loss of weight occurs (Bodola; see footnote 3).

There was no sexual dimorphism in the rate of growth or in the length-weight relation for 1,136 gizzard shad from Beaver Dam Lake, Ill. (Lagler and Van Meter, 1951: 357-360).

Abnormal growth has been reported by Hubbs and Whitlock (1929), who found two extreme forms in samples taken not far apart in the Arkansas and Poteau Rivers, Okla. The abnormal sample, composed only of young fish, showed a teratological condition (head long, wide, and swollen; eyes large; tails stunted) that was evidently related to an environmental factor or factors.

Size.—The gizzard shad is known to attain a total length of 20.5 inches but does not commonly grow longer than 10 to 14 inches. In a letter dated July 14, 1953, Alfred Larsen (Fishery Biologist, Pennsylvania Fish Commission) wrote that specimens of *Dorosoma cepedianum* killed in Presque Isle Bay early in 1953 (see section on Mortality) varied in length from 4 to 19 inches. Maturity may be attained at much smaller sizes than commonly thought, for Vladykov (1945: 35) reported a mature female to be 151 mm. (a little over 6 inches) in total length. Fish 10 to 13 inches long weigh about 1 pound; individuals 14 to 18 inches long, from the Ohio River drainage of Ohio, weigh 1 to 3 pounds; and the largest recorded specimen (20.5 inches) weighed 3 pounds 7 ounces (Trautman 1957: 182). As in other fishes, size and weight vary considerably and in some localities there is marked dwarfing.

Habitat and migration.—The gizzard shad inhabits large rivers, reservoirs, lakes, swamps, bays, borrow pits, bayous, estuaries, temporary floodwater pools along large river courses, sloughs, and similar quiet open waters which may be clear to very silty. Although it is fairly common in the relatively strong current of the upper Mississippi River, it prefers quieter waters and swarms in the sluggish lower parts of the same river. The adults may ascend smaller streams or ditches to spawn and the young are later abundant in such places if the gradient is sufficiently low. In coastal rivers of Virginia the young are present in great abundance well upstream from brackish water (Massmann 1953). In Lake Erie the species is most plentiful at the shallow western end, over mud bottom (Nash 1950: 563), particularly in protected bays and about the mouths of tributaries (Bodola; see footnote 3). Abundance is greatest in late summer and early fall when the populations are augmented by young-of-the-year. The species is particularly attracted by warm water flowing from industrial plants (see section on Mortality). It is able to withstand rather high temperatures, to 35° C., and has shown no geographic variation in its ability to tolerate lethal temperatures (Hart 1952: 28-29).

Gizzard shad are common in Chesapeake Bay only during the fall months, occurring principally in brackish water near the mouths of freshwater streams. The species is common or abundant in the rivers of the region throughout the year, but very young individuals evidently do not enter brackish water (Hildebrand and Schroeder, 1928: 106-108). Along the Texas coast, the species frequents the large, brackish-water bays where individuals may be taken throughout the year in waters that vary in salinity from 2.0 to 33.7 parts per thousand. Gizzard shad in this area prefer brackish water to sea water and, in general, the smallest fish occur in the freshest water, with size increasing as salinity increases (Gunter 1945: 30-31).

Dorosoma cepedianum is essentially an open-water species, usually living at or near the surface, and the young are reported to prefer beds of spatterdock (*Nuphar*) in Foots Pond, Indiana (Hubbs and Lagler, 1943: 77). In western Lake Erie, young shad live close to shore in midsummer, usually in shallow water (Bodola; see footnote 3). If the oxygen supply is adequate, the species may descend to depths as great as 108 feet, as in Norris Reservoir, Tenn. (Cady 1945: 113-114; Dendy 1945: 126; 1946a). In the Coosa River, Ala., gizzard shad were found in deep (25 feet) as well as shallow water (Scott 1951: 38-39).

Young-of-the-year gizzard shad travel in compact schools soon after hatching, but by fall most of the schools disperse and few form the following spring, at least in Norris Reservoir; schooling largely ceases by the time the shad are a year old (Dendy 1946b: 121). In the Chesapeake Bay region there is a fall "run" in September and October, and a corresponding spring "run" has been recorded in North Carolina. A spring migration, evidently a spawning run, has been noted in the Mississippi River near New Orleans, and lake populations migrate to shallower water at spawning time. An unusual midwinter migration was noted in the Minnesota River, from about December 1 until late January (Swanson 1932: 34).

Food.—Except for a short time after hatching, this species is almost entirely herbivorous, feeding heavily on microscopic plant life, phytoplankton, and algae.

At birth the alimentary canal is a simple, nearly straight tube (fig. 4, *a)* but by the time the wild fish is about 22 mm. long four flexures have developed; the section between the first and second flexures subsequently enlarges to become the gizzard and caeca arise from the duodenum by the 27.5-millimeter stage. The intestine becomes tremendously convoluted with age; whereas it equals about one-half the total length of the day-old fish, it becomes three times the length of the adult and is packed into an abdominal cavity only one-third that of the fish's length. The young commence to eat about 4 or 5 days after birth (Bodola; *see* footnote 3). Wier and Churchill (1946) have described the anatomy and histology of the digestive system.

During the first few weeks of life, gizzard shad eat mainly protozoa and entomostraca. Contents of the digestive tracts of larval and postlarval shad examined by Warner (see Wickliff 1945: 1-4) consisted almost entirely of water fleas *(Bosmina),* copepods, and a few ostracods. These organisms were found in young up to about 22 mm. long. Individuals 26 mm. long, with the intestine, gizzard, and liver well developed and having essentially the appearance of the adult, contained largely algal plankton (diatoms, desmids, and colonial forms) and shelled and flagellated protozoa *(Euglena),* which occur in the bottom ooze, on vegetation and as free-floating organisms. At this size, *Bosmina* has almost disappeared from the diet. Food may occur in the pharyngeal pockets, the gizzard, and the intestine (Bodola; *see* footnote 3).

The algal consumption of the gizzard shad led Tiffany (1922: 285) to describe these fish as "living tow nets." He identified 150 species and varieties of nonfilamentous algae from the stomach and intestine of specimens taken in streams and ponds of Ohio and Illinois. To what extent these are utilized as food is questionable, however, for Velasquez (1939) showed experimentally that 50 of the above species might have been viable after passing through the digestive tract. A certain amount of mud is typically ingested by the shad while feeding (hence the name, mud shad), but this material is evidently taken accidentally; however, sand may be purposefully ingested as an aid in the macerating action of the gizzard (Bodola; *see* footnote 3). On occasion, the species may be cannibalistic (Dendy 1946b: 119).

Earlier Tiffany (1921: 383) gave a summary of the food eaten by young shad in six Ohio lakes. This consisted of microalgae, 70 to 90 percent; microanimals, 0 to 15 percent; filamentous algae, 0 to 5 percent; and plant debris, 5 to 20 percent. Mud usually comprised from 10 to 30 percent of the stomach and intestinal contents, but it was often absent. The gizzard shad is able to utilize a large variety of microscopic plants and it does so consistently. Moreover, the diet is remarkably alike at various sizes (once the early zooplankton stage is passed). Tiffany found that the percentage composition of food eaten by shad 200 mm. long was not materially different from the data given above for young fish, except that there was more unrecognizable debris. Examination of intestinal contents in samples from Lake Erie showed that little food is eaten in winter and early spring (Bodola; *see* footnote 3).

In the vicinity of distilleries this species will feed on distillery slops (cornmeal) and it may also occasionally take Coleoptera, univalve mollusks, young *Corixa,* and spiders and water mites (Forbes 1888: 438; Forbes and Richardson, 1920: 47).

Seven specimens from Buckeye Lake, Ohio, 22 to 31 mm. in total length, taken on June 25 and July 11, 1930, yielded 14 percent Cladocera and 86 percent algae and debris (Ewers and Boesel, 1936: 61). Some of these individuals were in the transitional stage during which zooplankton is being replaced by phytoplankton in their diet.

Predators.—At a certain stage in its life history, the gizzard shad is reported to form a major part of the diet of at least 17 important game fishes. Of value in this respect are young-of -the-year about 2 to 5 inches long, but individuals 8 inches or longer are utilized to some extent by walleyes (*Stizostedion vitreum*), according to Stroud (1949). In ponds and lakes of Ohio, it is preyed upon by white bass (*Roccus chrysops*), largemouth bass (*Micropterus salmoides*), and white crappie (*Pomoxis annularis*) (Wickliff and Trautman, 1931: 15, 25, 37). In Foots Pond, Ind., the gizzard shad was eaten by three gars (*Lepisosteus platostomus*, *L. productus*, and *L. osseus*), white bass, largemouth bass, white crappie, and black crappie (*Pomoxis nigromaculatus*), according to Lagler, Obrecht, and Harry (1943: 120, 122-123, 126), and Lagler and Ricker (1943: 59-62). Two gars, *L. productus* and *L. osseus*, utilized the species in Texas (Bonham 1941: 359-360), and the skipjack (*Alosa chrysochloris*), northern pike (*Esox lucius*), yellow bullhead (*Ictalurus natalis*), and white crappie preyed upon the gizzard shad in Illinois (Forbes 1888: 435; Hansen 1951: 225). In the Illinois River, Forbes (1903: 34-38, 40) reported that walleye (*Stizostedion vitreum*), sauger (*Stizostedion canadense*), and yellow bass (*Roccus interruptus*) preyed upon shad between 3 and 4 inches long and that this species was a very important item in their diet.

In Norris Reservoir, Tenn., Dendy (1946b: 122, 124) stated that *D. cepedianum* constitutes the most important food supply for the game fishes. These are channel catfish (*Ictalurus punctatus*), largemouth bass, smallmouth bass (*Micropterus dolomieui*), spotted bass (*M. punctulatus*), black crappie, walleye, sauger, and the freshwater drum (*Aplodinotus grunniens*). In the Clinch River, Tenn., white bass and largemouth bass fed mostly on gizzard shad and brook silversides (Eschmeyer 1944: 38).

Even the lake trout (*Salvelinus namaycush*) is credited with eating *Dorosoma* in Cayuga Lake, New York. An examination of 312 stomachs that contained food revealed one with a gizzard shad 6.7 inches long.[5] The bowfin, *Amia calva*, also is known to eat gizzard shad (Lagler and Hubbs, 1940).

The periodic mortality (see elsewhere) of gizzard shad provides an important source of food for numerous species of waterfowl. This food comes at a most opportune time, when other foods are scarce or when waterfowl are forced out of their normal feeding places by hunters. Young-of-the-year shad are fed upon at Buckeye Lake, Ohio, during the fall and winter by the lesser loon, horned grebe, pied-billed grebe, white pelican, great blue heron, American egret, snowy egret, eastern green heron, black-crowned night heron, American merganser, red-breasted merganser, hooded merganser, mallard, black duck, gadwall, baldpate, green-winged teal, blue-winged teal, American pintail, wood duck, redhead, canvasback, lesser scaup, ring-necked duck, American goldeneye, bufflehead, oldsquaw, king eider, American scoter, and whitewinged scoter (Trautman 1940: 110-111, 155-206). During the relatively open winter of 1952-53 at Columbus, Ohio, Trautman (personal communication) stated that the huge waterfowl concentrations in central Ohio would have been impossible without the gizzard shad.

Utilization.—The gizzard shad is not esteemed for food by man because of its soft and rather tasteless flesh and the numerous fine bones. There is no evidence that the aborigines sought this species (Rostlund 1952: 14). In the Chesapeake Bay region it once sold fairly well to a class of trade that demanded a cheap fish. In 1921, the retail price in Baltimore was about 5 cents a pound. Among the commercial fishes of Chesapeake Bay in 1920, it ranked twentieth in value with a catch of 72,852 pounds worth $2,013 (Hildebrand and Schroeder, 1928: 107). The commercial catch in the Great Lakes over a 14-year period (table 4) shows the erratic nature of the take.

[5] Galligan, James P., The distribution of lake trout and associated species in Cayuga Lake. M.A. thesis, Cornell University, 1951: 72.

TABLE 4.—*Commercial catch of* Dorosoma cepedianum *in the Great Lakes, 1939-57*

[Excluding Lake Superior. From statistical records of U.S. Fish and Wildlife Service and Michigan Department of Conservation]

Year	Lakes	Pounds [1]	Value [1]
1939	Huron	300	$18.00
1940	Erie, Huron	35	1.00
1941	Huron	300	6.00
1942	Erie (Pa.)	23,000	139.00
1943	Erie, Huron	900	44.00
1944	do	300	13.00
1945	do	600	28.00
1946	Huron	100	7.00
1947	Erie, Huron	600	10.00
1948	Huron	29,400	294.00
1949	Erie, Huron	31,600	930.00
1950	do	20,600	614.00
1951	do	450	16.00
1952	do	2,300	55.00
1953	Huron	100	1.00
1954	Ontario, Erie. Huron	2,200	32.00
1955	Huron, Michigan	3,700	41.00
1956 [5]	do	5,180	149.00
1957 •	do	4,750	95.00
Total		126,415	2,493.00

To nearest round figure.
[3] For State of Michigan only; final figures for 1957 are approximate.

The species has been used to some extent in making guano, and in 1874 a guano factory existed at Black Point, above Palatka, Florida (Bean 1893: 64; Goode 1884: 610). Many years ago, on Lake Erie, it was split and salted and sporadically marketed with other low-grade fish as "lake shad" (Jordan 1882: 871), and in the 1840's it appeared on the markets in Ohio but was not highly regarded (Kirtland 1838: 195).

When it becomes excessively abundant, as it did in Black Hawk Lake, Iowa, in 1951, the gizzard shad may be used as hog food or for field fertilizer (Madden 1951: 185). In the Ohio waters of Lake Erie, the harvest is limited and is restricted to Sandusky Bay. Here one commercial drag seiner takes shad, carp, and goldfish for use as hog feed, and another drag seiner provides enough *Dorosoma* to freeze for trout food (letter from Robert Cummins, Jr., Sandusky, Ohio, June 26, 1953). In the Pennsylvania waters of Lake Erie, where shad mortality has been high in recent years, the species has been steamed and pressed for oil and the remainder used as cattle food. Gizzard shad roe has occasionally been marketed for food in Florida (Moody 1954: 147). Its use as food for fur animals has been investigated. Since the whole fish contains considerable amounts of the enzyme thiaminase, it must be cooked or fed in a special feeding schedule. Protein content of the whole fish is about 15 percent and fat content 12 percent, which is comparatively high (U.S. Fish and Wildlife Service, 1956).

The species has had limited use as a bait fish. Evermann (1899: 308) claimed that gizzard shad were "of considerable importance as bait" in the Atchafalaya River, Miss., but Kuhne (1939: 25) stated that since it dies very easily it is an unsatisfactory bait minnow. According to T. H. Bean (1893: 64) , the shad "has been very successfully kept in the aquarium * * *." It has also been successfully propagated in ponds as food for young bass.

Although the gizzard shad can hardly be classed as a sport fish it is taken occasionally by angling, as at Lake Chautaqua, Ill. A hook baited with an angleworm, a small minnow, or even an artificial fly, is attractive to the shad, and Abbott (1861: 366) stated that the fish afforded much sport to juvenile anglers in New Jersey.

Abundance.-In recent years, the gizzard shad has become a problem species wherever it has so increased that a detrimental affect is produced on other fishes. *Dorosoma* has inhabited Lake Erie for more than 100 years, yet its greatest abundance there has been attained since about 1950, according to commercial fisherman (Bodola : *see* footnote 3) . Fluctuating but generally increasing numbers in the Great Lakes, especially Lake Huron and Lake Erie, is indicated by the commercial catch from 1939 to 1957 (table 4). In 1948, 3,000 pounds were taken in one seine haul in Lake Huron, and it was noted that the fish were being captured in record numbers after a 15-year lull in abundance (Ann Arbor News, Mich., December 1, 1948). Overpopulation is typically associated with manmade modification of the environment (Lagler and Van Meter, 1951).

In Carpenter Lake, Ky., during October 1954, 285 pounds of gizzard shad per acre were killed with rotenone in an impoundment of 70 acres having an average depth of 5 feet and a maximum depth of 11 feet ; only about 50 pounds of shad per acre were anticipated (Bowers 1955). Among forage fishes, there was a phenomenal increase in abundance of gizzard shad in Clearwater Lake, Mo. The percentage composition rose from 2.0 in 1949 (1 year after impoundment) to 57.8 in 1950; large schools of shad were seen in 1950 throughout the lake (Martin and Campbell, 1953: 59). Since the species had spawned before the reservoir filled in 1948, the tremendous increase in 1950 resulted largely from brood stock spawned in 1949.

Black Hawk Lake, Iowa, became so overpopulated with Dorosoma that the game fishes were suppressed by sheer weight of numbers of gizzard shad (Madden 1951). In 1934 there was a complete winter kill in this shallow, fertile lake of 957 acres ; in 1939, 105 acres were dredged so as to avoid further severe winter mortality. The depth was 6 to 7 feet except in the dredged portion, which was 9 to 16 feet. The first gizzard shad was netted in 1945 and by 1947 (when the lake was flooded by Boyer River) the population had reached a nuisance level. With the progressive increase of shad it was noted that bottom organisms declined. In the fall and winter of 1950-51, 10,000 adult *Dorosoma* were removed by seining. Largemouth bass, walleye, and northern pike were stocked in 1951 to provide predators to keep the shad in check, but in the fall of 1951 approximately 7,360 young gizzard shad per acre were removed from the lake. Nevertheless, through intensive netting during the period 1951-57, the poundage percentage of gizzard shad removed per haul (mostly by a 2,500-foot seine) decreased from 98.1 to 2.8; at the same time the poundage percentage for carp increased from 1.8 to 96.3—thus suggesting that the ecological niche vacated by the shad was rapidly assumed by the carp (Rose 1957).

Increase of gizzard shad in 31,000-acre Lake Apopka, Fla., reached the point (sometime between 1950 and 1956) where this species constituted more than 80 percent of the total fish population (Heinen 1958). By means of selective treatment with rotenone, an estimated 3.5 million pounds of Dorosoma were killed (November 4, 1957) in the first of three projected applications. Past records indicated a marked decrease of sport fishing after 1950 and a change in the lake from clear water and large quantities of submerged vegetation to turbidity (from high plankton bloom) and sparse submerged plants. Similar overpopulations of gizzard shad have occurred in other Florida lakes. For example, in Newnans Lake, Alachua County, with 6,182 acres, an estimated 1 million pounds of shad were destroyed with rotenone (Melvin T. Huish, personal communication). In five of seven shallow Florida lakes studied by Moody (1954), gizzard shad and gars constituted about 50 percent or more of the total weights of fishes obtained by large haul seines.

In comparing fish populations in two similar Oklahoma lakes, Jenkins (1957) demonstrated that the lake containing gizzard shad had an estimated standing crop of 1,043 pounds per acre and a weight of desirable-sized fish of 466 pounds per acre, whereas the lake lacking this species had an estimated standing crop of 655 pounds per acre of which 608 pounds comprised desirable-sized fish. The average coefficient of condition for six species of sunfishes in the two lakes showed that the lake without shad was above the State average, whereas that containing Dorosoma was well below the State average. This is indicative of direct competition between centrarchids and gizzard shad in small-lake populations.

Parasites.—This species appears to be usually free from attack by parasites, from which it is undoubtedly protected by its herbivorous food habits. Bangham and Hunter (1939: 396) examined 5 gizzard shad from Lake Erie and found an unidentified larval nematode in the intestine of one young specimen. Van Cleve found but two species of Acanthocephala in 300 gizzard shad, and Essex and Hunter reported no parasites in more than 100 individuals from the Rock and Mississippi rivers (as cited by Bangham and Hunter). In Buckeye Lake, Ohio, where gizzard shad are abundant, the young often carry a very heavy infestation of a myxosporidian which forms large white cysts in the body cavity. Each of 15 adult shad from the same lake were free of parasites, and 10 of 12 young carried many of the encysted sporozoans (Microsporidia) described above, often giving them a "potbellied" appearance (Bangham 1941).

Mortality.—Many gizzard shad die during the winter, frequently in great numbers (Wickliff 1953). This is a rather regular and often spectacular phenomenon and on occasion may lead to a health problem, as it did when more than 1,000 tons of dead and live Dorosoma were removed from Lake Erie at Erie, Pa., during January and February 1953 (Walsh 1953: 2-4, 5 figs.). The mass mortality, which occurred in Presque Isle Bay, was the greatest in a sequence of similar deaths that took place there during the decade 1943 to 1953. The bay contains two basins, East and West, each of which has an area of about 15 acres, with a maximum depth of 8 to 10 feet. The pumping of water from the East Basin to the West Basin by an electric power company resulted in a discharge of warmed water into the West Basin at a rate greater than 100,000 gallons per minute. At the time of the mass deaths, water in the West Basin varied from 55 to 60° F., whereas that in the East Basin and the bay proper was only 34-35° F. Dissolved oxygen was not low and, with one exception, carbon dioxide levels were not unusual. The mortality occurred in the warmer West Basin and was clearly associated with high temperature. In 1950, the previous record year, 800 tons of shad were removed from the same basin (I am indebted to Alfred Larsen, Fishery Biologist, Pennsylvania Fish Commission, for most of the foregoing information).

The cause of such mortalities is not completely understood. It has been suggested that a marked difference between the carbon dioxide tension of the surface water and the carbon dioxide partial pressure of the air is a causal factor (Powers 1938: 279). This has been disputed, for example by Baker (1942: 48), and it is generally felt that abrupt temperature changes cause the mass deaths of this species (see also Agersborg 1930). This factor was noted more than 100 years ago by Kirtland (1844: 237), who described a mass mortality of *Dorosoma* in the Miami Canal, Ohio, after an abrupt warming following prolonged cold weather. Kirtland, however, did not realize that the deaths were probably a direct result of the sudden temperature rise, for he attributed the mortality to an inability of the species to withstand the colder, northern climate. That low temperature is a factor limiting the distribution of the gizzard shad, however, is evidenced by their absence from the upper parts of Lake Huron and Lake Michigan and all of Lake Superior (Miller 1957: 108). Also, large numbers of young shad were seen frozen in the ice throughout Fort Randall Reservoir, S. Dak., during the winter of 1955-56, a mortality plausibly attributed to cold temperature (Shields 1956: 29).

The possibility that a fungus disease may be locally responsible for deaths of gizzard shad (Trautman, in Clark 1942: 255; also suggested to me in personal communication by Dr. George W. Bennett) seems to me to be more likely the result of secondary infection after the shad are weakened. Bangham and Hunter (1939: 396) and Bangham (1941: 442) suggested that a sporozoan parasite may kill many young gizzard shad during August and September in Buckeye Lake, Ohio. However, the shad that die are represented by several year classes, indicating that the causal factor (or factors) is not necessarily correlated with age.

The gregarious habits of this species and its predilection for quiet waters may also lead to mass mortality. From about November 11 to 13, in 1952, a large run of shad from the Detroit River up the intake pipe (diameter, 5 feet) of the Parke-Davis Company plant in Detroit led to the death, from mechanical causes, of an estimated 2 to 3 tons of *Dorosoma* of rather uniform size. The reduced current velocity of the intake, as compared with that in the river, is a plausible explanation for the migration (summarized from report in the files of the Institute for Fisheries Research, Michigan Department of Conservation).

There are two reports of apparent mass spawning mortality, both from Florida (Moody 1957: 30). A marked reduction of the population, without subsequent immediate recovery, occurred in April or May toward the end of the spawning season. A similar mortality took place in the threadfin shad (*D. petenense*) in Florida (Berry, Huish, and Moody, 1956).

Forage value.—Since the 1880's when its food and feeding habits were first studied by Forbes, the merits of the gizzard shad as a forage fish have been repeatedly emphasized. Its important qualifications are (1) direct utilization of phytoplankton ; (2) a high reproductive capacity and abundance; (3) general freedom from parasites ; (4) a rapid rate of growth ; and (5) utilization as food by important game fishes. It has been spoken of as "the most efficient biologically of all the forage fishes" (Hubbs 1934: 57) because of the short and efficient link in its food chain that directly connects basic plant life with game fishes.

Thus, it might seem as if the gizzard shad could be called the ideal forage fish, but its suitability in this regard is affected by certain ecological conditions. Because of rapid growth to a size not eaten by predators ample breeding stocks of *Dorosoma* are assured, but undue multiplication of these stocks may result in competition with the predators. The heavy populations of gizzard shad in some waters may be partially responsible for high turbidity and this may lead to a decrease in productivity of game fish (Thompson 1941: 211, 214). The great abundance of young shad may result in competition for food with the young of game fishes. Illustrations of how shad populations can mushroom in warm, shallow bodies of water that have a soft mud bottom, high turbidity, and relatively few predators have already been given (see section on Abundance, p. 384). Here *Dorosoma* finds conditions for existence at an optimum and the introduction of this fish into such waters is to be avoided if a high level of game-fish production is desired. Wiebe (*in* Hubbs 1934: 60-61) noted that stocking gizzard shad in ponds at Burlington, Iowa, resulted in overpopulation of the species.

In many other waters the gizzard shad is a highly esteemed forage fish. Wickliff (1933: 275) stated, "Upon the presence or absence of this fish seems to rest the burden of whether or not impounded waters in Ohio will be productive of several game fish * * *." This author pointed out that *D. cepedianum* does not compete appreciably with other fishes in spawning sites or in general habitat preference, that it cannot be depleted by angling, and that it makes an attractive bait. Its chief drawbacks are a natural mortality in the spring and fall and sensitivity to handling. In the deep, clear reservoirs of the Tennessee River system, young-of-the-year gizzard shad constitute the most important food source of the game species taken from deep as well as from shallow water. Continuous cropping of this year class leaves just a sufficient nucleus of adults to maintain a large number of young, so that the forage fish–predator relation is in nearly perfect balance.

In experimental combinations of gizzard shad with bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) in Alabama ponds, Swingle (1949: 53-55) showed that although a relatively high poundage of largemouth bass resulted from a shad–bass combination, the yield was not sufficient to justify omission of bluegills and, when that species was added, large shad accumulated and reduced the size of the adult bluegills with which they competed for food.

In discussing the management of Indiana ponds for fishing, Krumholz (1952: 256) wrote that gizzard shad should not be stocked in the ponds of that State, but gave no reasons.

The gizzard shad is said to be by far the most abundant species in the larger impoundments of Oklahoma and to assure an ample food supply for game fishes throughout the summer months (Jenkins 1951: 93). The species is fast-growing and rather short-lived, and, although its rapid growth eliminates the gizzard shad from a size range suitable for food of the smaller game fishes, the large crop produced each year offsets this disadvantage (Jenkins 1953b: 36).

After a study of 22 warm-water artificial lakes in Illinois, Bennett (1943: 364) wrote :

> Gizzard shad were present in 10 of the 22 lakes. In some cases they were introduced by floods from nearby streams. In others they were stocked as forage fish. They are not satisfactory for this purpose in artificial lakes because they reproduce in tremendous numbers and rapidly become too large to be eaten by the game fish present. In almost every case, large shad populations were associated with small numbers of bass. In 5 of the 10 lakes the shad constituted from 48 to 65 percent of the entire fish populations (by weight) and the game and pan fish were small and stunted.

Dorosoma cepedianum is a valuable forage fish but under certain conditions it is not suitable for this purpose. In shallow, warm-water lakes with mud bottom, high turbidity, and high fertility, it is likely to get out of control, even if numbers of predatory game fishes are present. This is particularly true if the species is not native to such waters. It is ideal for forage use in fluctuating impoundments (such as Norris Reservoir, Tenn.) where the water is deep and clear, the shoreline is abrupt, no littoral vegetation develops, there is a paucity of benthic flora and fauna but adequate plankton, and sufficient predatory species are present to crop the young-of-the-year. It is also valuable in many waters that are somewhat intermediate between these two extremes, particularly where it forms a part of the native fish fauna which also includes a number of predatory fishes.

Range.—A detailed discussion of the northern limit of the gizzard shad was published recently (Miller 1957: 105-108). However the species may have entered the Great Lakes, it is known today from Lake Erie, the southern parts of Lake Huron and Lake Michigan (which it has very recently invaded), and the Lake Ontario basin (Greeley 1940: 68). Specimens were taken recently in the St. Lawrence River near Quebec (Vladykov 1945). The erroneous records of this species from New Brunswick have been further discussed by Scott and Crossman (1959: 30).

The species ranges from southeastern South Dakota and central Minnesota, the Great Lakes drainage, and extreme southern New York, southward through the Mississippi River system and along the Atlantic slope to the Gulf coast of the United States and to the basin of the Rio Pánuco in eastern Mexico.

That the species has also entered the artificial canals and thus extended its range seems well founded. It has entered Lake Michigan by moving through the Chicago River Canal, and its occurrence at the northern end of Cayuga Lake, N.Y., has been plausibly credited to its transport there from Lake Erie by way of the Erie Canal. Wright (1918: 544) wrote, "The most recent Erie contribution in the mouths of our Ithaca streams is the gizzard shad (*Dorosoma cepedianum*) * * *s." Greeley (1928: 95) recorded about 20 specimens taken November 11, 1916, from Cayuga Lake (evidently the same fish referred to by Wright), with the notation that fish presumably of this species were reported to have come through the Erie Canal one winter, many dying under the ice.

SUMMARY

Because of its importance to fishery workers, the gizzard shad, *Dorosoma cepedianum,* is treated in detail. Series of specimens from throughout its wide range form the basis for a summary of taxonomic characters and variation ; no subspecies are recognized.

Dorosoma cepedianum spawns near the surface in fresh water from about the middle of March to the latter part of August, over a water temperature range of about 50° to 70° F. The eggs are sticky and demersal and, at times, may cover aquatic plants. The fertilized egg is nearly transparent and measures about 0.75 mm. in diameter after fixation. The embryology and early life history are described and figured.

The gizzard shad usually matures in its second or third year and may live to be 10 years old, but it typically does not attain an age greater than 5 to 7 years. In the northern part of its range, it may mature at about 6 inches in total length. From 70 to 80 percent of its annual growth occurs during June—August or July—September, depending on the season and the age of the fish. Fish 10 to 13 inches long weigh about 1 pound. The species commonly attains total lengths between 10 and 14 inches; the largest known individual was 20.5 inches long and weighed 3 pounds 7 ounces. No sexual dimorphism has been demonstrated for growth rate or in the length-weight relation. There are no reliable external characters by which the sexes may be distinguished.

Except for a few weeks after hatching, *D. cepedianum* is almost entirely herbivorous, feeding heavily on microscopic plants, phytoplankton, and algae. Once the early zooplankton stage is passed the diet is remarkably alike at various sizes. The species is essentially a filter feeder.

At least 17 important game fishes may eat gizzard shad, usually the young-of-the-year about 2 to 5 inches long; walleyes, however, may utilize individuals 8 inches or longer. Its importance as a forage fish is emphasized by the short food chain (direct utilization of phytoplankton), high reproductive capacity and abundance, general freedom from parasites, and rapid growth rate. At times, however, the species so overpopulates some waters that expensive means of control are necessary. Gizzard shad may become a nuisance in warm, shallow lakes that have a soft mud bottom, high turbidity, and relatively few predators; this is particularly true if the species is not native to such waters. In many other waters the gizzard shad is a highly esteemed forage fish, and it is particularly valuable for this purpose in fluctuating inpoundments which have deep and clear water, an abrupt shoreline, little or no littoral vegetation, adequate plankton (but a sparse benthic flora and fauna), and sufficient predatory fishes to crop the young-of-the-year.

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