BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 15 Number 3

ATLANTIC AND GULF OF MEXICO MENHADENS, GENUS BREVOORTIA (PISCES: CLUPEIDAE)

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Gainesville

1970

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

Communications concerning purchase or exchange of the publication and all manuscripts should be addressed to the Managing Editor of the Bulletin, Florida State Museum, Seagle Building, Gainesville, Florida 32601.

Published 5 June 1970 Price for this issue $1.30

ATLANTIC AND GULF OF MEXICO MENHADENS, GENUS *BREVOORTIA* (PISCES: CLUPEIDAE)

MICHAEL D. DAHLBERG[1]

SYNOPSIS: Western North Atlantic menhadens, genus *Brevoortia,* comprise two well-defined groups, four species, several races, and two hybrid combinations. One group, the large-scaled menhadens, live in temperate waters and are represented by *B. tyrannus* in the Atlantic Ocean and *B. partonus* in the Gulf of Mexico. *B. tyrannus* occurs in the Atlantic from Nova Scotia to Jupiter Inlet, Florida. Populations include a spring-spawning race north of Long Island, N.Y., an autumn-spawning race on the coast between Long Island and North Carolina, and a winter-spawning race in the Indian River area of Florida. Evidence also indicates the existence of a southern Atlantic population that ranges from North Carolina to northeast Florida. *B. patronus* ranges from southwest Florida along the gulf coast to Veracruz, Mexico. The large-scaled manhadens support the fish oil and fish meal industry of the Atlantic and gulf coasts of the U.S.

The small-scaled menhadens are limited to warm-temperate waters. An Atlantic population of *B. smithi* is known from North Carolina to Jupiter Inlet, Florida. A gulf population of *B. smithi* ranges from Florida Bay to Louisiana. The western gulf cogriate, *B. gunteri,* occurs between Louisiana and the Gulf of Campeche and may extend into the Caribbean.

Two hybrid combinations are known. *B. smithi* x *B. tyrannus* ranges on the Atlantic coast from Sapelo Island, Georgia, to Jupiter Inlet, Florida. *B. smithi* x *B. patronus* ranges on the gulf coast from Florida Bay to Port St. Joe, Fla. Evidence is presented that *B. tyrannus* in the Indian River of Florida is modified by introgression.

This study presents a key to the menhaden species and hybrids, describes the various forms, presents synonymies and recent references, and discusses hybridization, geographic variation, population structure, and zoogeography.

[1]Contribution 192 from the University of Georgia Marine Institute. This study was part of a dissertation submitted to the Graduate School of Tulane University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The author is currently Research Associate with the Marine Institute, University of Georgia, Sapelo Island, Georgia 31327, and Assistant Professor in the Zoology Department, Athens, Georgia 30601. Manuscript received 5 April 1969—Ed.

Dahlberg, Michael D. 1970. Atlantic and Gulf of Mexico Menhadens, Genus *Brevoortia* (Pisces: Clupeidae). Bull. Florida State Mus., vol. 15, no. 3, pp. 91-162.

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INTRODUCTION

Menhadens, genus *Brevoortia,* are marine and estuarine fishes of the family Clupeidae. This large family is composed of about 70 genera and 150 or more species that occur in all seas of the world except those of the antarctic region (Hildebrand, 1963). Menhadens and other clupeids such as herrings occur in large schools and are important commercially. Although herrings are food fishes, menhadens are used almost entirely for the production of fish oil, fish meal, and water solubles, and support a major fishery on the U.S. Atlantic and Gulf of Mexico coasts.

The New World genus *Brevoortia* Gill according to Hildebrand (1948) contained seven species in the western Atlantic. His posthumous (1963) paper treats their systematics similarly, recognizing seven species, five of them limited to North America. One of these (*brevicaudata*) is not valid. *B. pectinata* Jenyns and *B. aurea* (Agassiz) occur on the Atlantic coast of South America (Hildebrand, 1963). De Buen (1958) erroneously placed in *Brevoortia* two species of *Ethmidium* Thompson that occur on the Pacific coast of South America.

Of the North American menhaden species, two are large-scaled and have their centers of abundance in temperate waters. *B. tyrannus* occurs in the Atlantic Ocean and *patronus* in the Gulf of Mexico. Two species are small-scaled and their populations are centered in warm-temperate waters. *B. smithi* Hildebrand occurs on the southeastern U.S. coast and in the eastern Gulf of Mexico. It is most abundant on the Florida coasts, but is probably discontinuous off southeastern Florida. *B. gunteri* occurs in the western Gulf of Mexico and overlaps *smithi* off Louisiana. Extensive hybridization occurs between the two species found on each of the Florida coasts.

Hildebrand (1963) did not have available many critical series used in this study, including those of *tyrannus, smithi,* and hybrids from the central Atlantic coast of Florida, and *patronus* and hybrids from the gulf coast of peninsular Florida. He did not consider certain important characters, such as frontal groove, gill filaments, and melanin on the anal fin, and he did not exploit others completely. Hildebrand (1948) mentions certain geographic changes in *tyrannus* but gives no data to substantiate his conclusions.

Several types of systematic problems occur in this group. One is the taxonomic status of closely related allopatric forms. I prefer not to change a binomial to a trinomial when the populations are allopatric, their statuses are controversial, and it is not proved to what level speciation has occurred. Ability to interbreed does not prove populations to be subspecies, because the markedly different large-scaled and small-scaled menhadens interbreed, but the sex ratio of hybrids may be useful. Another situation occurs with the two closely related species of small-scaled menhadens that are sympatric but markedly different. This study also attempts to define races of menhaden. Finally the presence of an undescribed form off eastern Florida (Reintjes, 1960) stimulated the analysis of two hybrid forms on the Florida coasts.

Acknowledgments

This problem was studied under the guidance of Royal D. Suttkus whose assistance and financial support made possible its completion. Assistance was provided through his National Institutes of Health Grant, Number 5-T01-00027-03. Additional funds were obtained from the Society of Sigma Xi RESA Research Fund.

For the loan of the specimens I wish to thank Richard Baldauf of Texas A and M University, J. Y. Christmas and Gordon Gunter of the Gulf Coast Research Laboratory, John Finucane of the Bureau of Commercial Fisheries Laboratory at St. Petersburg Beach, Ernest A. Lachner of the United States National Museum, Martin Moe of the Florida State Board of Conservation, C. R. Robins of the Institute of Marine Science at Miami, Ralph W. Yerger of Florida State University, and Donald C. Scott of the University of Georgia. Specimens were also borrowed from the Bureau of Commercial Fisheries Laboratory at Galveston, Texas, the Institute of Marine Science of Texas, and the University of Florida. Additional series were contributed by John Reintjes of the Bureau of Commercial Fisheries Laboratory at Beaufort, N.C., and by my grandfather, A. P. Miller.

C. Richard Robins and other members of the Institute of Marine Science of the University of Miami allowed me to sort and analyze valuable juvenile menhadens from shrimp collections made in Florida Bay.

Most of the specimens were originally collected by commercial fishermen, many of whom saved specimens for this study. Thanks are extended to: J. Howard Smith Co., N.J.; Seashore Packing Co., Beaufort, N.C.; Exteen Corbett, Nassau Fertilizer and Oil Co., Inc., Mayport, Fla.; Kitchel's Fish Co., Eau Gallie, Florida; Don Sembler, Sembler's Fishery, Sebastian, Fla.; Summerlin's

Baywood Fishery at Fort Pierce, Fla; Guy Freeman at Jupiter Inlet, Fla.; Wally Dickinson, Naples Packing Co. at Everglades, Fla; Gasparilla Fish Co. at Placida, Fla.; Capo Fish Co. at Cortez, Fla.; Brown's Fishery at Horseshoe Beach, Fla.; Gulf Stream Crab Co. at Steinhatchee, Fla; "The Barn" Fish Market at Carrabelle, Fla.; Millender and Son Fish Co. at Carrabelle, Fla.

I am grateful to my thesis committee (R. D. Suttkus, A. E. Smalley, A. A. Arata, M. Mizell) and fellow students (John S. Ramsey, Kenneth Relyea, and Richard Daly) for assistance. Frederick H. Berry of the Tropical Atlantic Biological Laboratory at Miami, Florida, was helpful because of his constant interest in the problem and vast knowledge of clupeid fishes. Edward C. Raney, Ernest Provost, and John Reintjes kindly criticized the manuscript.

Methods

I gathered numerical data from approximately 1,000 specimens and examined additional specimens for field identification characteristics and gonadal maturity. Numbers of specimens in collections and size range of specimens examined are listed in "Material".

Abbreviations used for collections are as follows:

BCFG—the Bureau of Commercial Fisheries at Galveston, Texas.
BCFSP—Bureau of Commercial Fisheries at St. Petersburg Beach.
FSU—Florida State University at Tallahassee.
GCRL—Gulf Coast Research Laboratory.
TAMU—Texas A. and M. University.
TU—Tulane University.
TIMS—Texas Institute of Marine Science.
UF—University of Florida.
UG—University of Georgia.
USNM—United States National Museum.

Descriptions are based on selected material examined personally. Only larger specimens (referred to as adults below) are used in descriptions except for large juveniles of *smithi* and *smithi* x *patronus*, both from Florida Bay, from which meristic data are included. Specimens referred to as adults are over 147 mm standard length; juveniles are less than 142 mm. The descriptions apply to juveniles, except for characters that change with growth, such as body proportions, body color (in large-scaled menhadens), gill rakers, gill filaments, opercular striations, and pseudobranchiae. Large adults are used for statistical comparison of proportions with one exception: shorter adult *tyrannus* from Chesapeake Bay, North Carolina, Fernandina Beach, and Indian River, Florida are compared. These shorter specimens are not compared with longer specimens. Meristic and proportional differences regarded as significantly different are below the 5 per cent level (nonoverlap of two standard errors of two samples) except when stated otherwise.

Meristic data in the descriptions are presented as the usual range of variation followed by the total range in parentheses. Because gill raker numbers increase with size of fish, they are plotted against standard length. Proportional data are presented as the range of the sample means followed by total range of variation in parentheses. A sample of *patronus* from Suwannee is tabulated for Steinhatchee to facilitate comparisons.

Synonymies are restricted to primary references. Recent references on the ecology and systematics are also given. Much menhaden literature published after Hildebrand's (1948) treatise was not cited in his 1963 posthumous treatise. In view of bibliographies by Reintjes (1964b) and Reintjes *et al.* (1960) and a literature review by Gunter and Christmas (1960), my reference lists for *tyrannus* and *patronus* are limited to papers published after 1960. References that pertain to all four North Atlantic species are listed only under *tyrannus*.

Proportions are expressed as per cents of standard length. Standard length was determined by dissection because the tail does not bend at the posterior end of the hypural plate, but at a point anterior to it as Berry and Barrett (1963) found in *Opisthonema*. Measurements and counts were made as prescribed by Hubbs and Lagler (1958) and Hildebrand (1948) except as listed below.

LATERAL SCALE ROWS.—The number of oblique scale rows counted from the posterior edge of the operculum to the caudal fin base. Scale rows are often indistinct in the small-scaled species and in hybrids; successive counts on the same individual often vary slightly.

PREDORSAL SCALES.—The number of modified scales anterior to the dorsal fin are counted as the total number on the left side. Hildebrand (1963) counted only those with a free lateral edge.

VERTEBRAE.—I follow June (1958, 1965) and do not include the hypurals in vertebral count. Hildebrand (1963) and Christmas and Gunter (1960) counted the hypurals as one vertebra.

ANAL RAYS AND DORSAL RAYS.—Only those that are branched or transversely split to any degree are counted. Principle ray counts are usually one unit higher.

GILL FILAMENTS ON CERATOBRANCHIAL ARCH.—The number in the outer row of filaments on the first ceratobranchial gill arch. This count increases slightly with body length.

GILL RAKERS.—The number on the lower arch (hypobranchial and ceratobranchial).

OPERCULAR STRIATIONS.—I count only those at the base of the opercle posterior to the vertical groove present at the anterior edge of the opercle.

Head length.—Measured from the tip of the snout to the posterior edge of the bony opercle, not to soft margin.

Head depth.—Measured from the occiput to the junction of the first two ventral scutes.

Frontal groove.—This groove, located above the suture of the frontal bones, is categorized as follows: (A) absent, (B) present but reduced in length or discontinuous, (C) present as a long thin slit or well developed groove; in category C it extends the entire length of the frontal groove suture.

Ventral fin.—The relative lengths of the inner, middle, and outer rays when the fin is folded are categorized as follows: (A) inner and middle rays considerably shorter than outer rays, inner rays about one-half to two-thirds the length of the fin; (B) inner and middle rays slightly shorter than the outer rays; (C) inner rays shorter than outer rays but middle rays are equal to or longer than the outer rays; (D) inner rays are equal to outer rays and the fin is rounded; (E) inner rays are slightly longer than outer rays.

Lateral spots.—Scattered black spots located along the side of the body, but not including the shoulder or humeral spot.

Darkness of anal fin.—That visible to the naked eye, categorized as follows: (1) absent, (2) a few scattered melanophores, (3) dusky but not black; (4) blackish on at least the anterior half of the fin.

Yellow pigment on body, anal fin, and ovaries.—The relative intensity of xanthin, which fades quickly after preservation.

Key to Menhaden Species and Hybrids

1A. Ventral fin with inner rays, or at least middle rays, as long as outer rays (especially south of North Carolina). Frontal groove well developed. Lateral spots usually present at and below the level of the humeral spot. Opercular striations usually 13-27. Scale pectinations pointed. Scales large. Lateral scale rows usually 42-53. Predorsal scales usually 29-44. Gill filaments usually 44-64. Annal fin usually dusky or black. —2

2a. Atlantic Ocean. Gill filaments on ceratobranchial arch usually 53-64. Vertebrae usually 46-48. Total predorsal scales usually 35-44. Ventral scutes usually 31-34.

B. tyrannus

2b. Gulf of Mexico. Gill filaments on ceratobranchial arch usually 44-54. Vertebrae usually 44-46. Total predorsal scales usually 29-37. Ventral scutes usually 29-31.

B. patronus

1B. Ventral fin with inner rays considerably shorter (about 1/2 to 2/3) than outer rays and outer margin normally straight. Frontal groove absent. Lateral spots lacking (except for two adult specimens examined from the gulf coast of Florida with a single lower row). Opercular striations usually 0-13. Scale pectinations rounded. Scales small. Lateral scale rows usually 55-74. Predorsal scales usually 39-53. Gill filaments usually 39-47. Anal fin usually not dusky except in northeastern Gulf of Mexico. —3

3a. Vertebrae usually 44 or 45. Scutes usually 30-32. Scales between tip of pectoral and base of pelvic usually 3-5. Head and jaws smaller, the head depth usually 26-29%, head length usually 28-30%, upper jaw usually 12.5-14.0%, and mandible usually 15.0-17.0%.

B. smithi

3b. Vertebrae usually 42 or 43. Scutes usually 28-30. Scales between tip of pectoral and base of pelvic usually 1 or 2. Head and jaws larger, the head depth usually 29-32%, head length usually 31-33%, upper jaw usually 14.5-16.5%, and mandible usually 17.5-20.0%.

B. gunteri

1C. Ventral fin usually with both inner and middle rays slightly shorter than outer rays (87% of Atlantic hybrids and 83% of gulf hybrids). Frontal groove usually reduced in length (59% of Atlantic hybrids and 71% of gulf hybrids) but may be absent or well developed. Lateral spots usually absent or present only in a lower row. Opercular striations usually 10-22. Scale pectinations usually pointed. Scales large. Lateral scale rows usually 42-59. Predorsal scales usually 34-47. Gill filaments on ceratobranchial arch usually 38-50. Anal fin usually dusky or black.

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4a. Lateral spots usually absent. Lateral scale rows usually 44-59. Predorsal scales usually 36-47. Atlantic coast of Florida.

Hybrid *B. smithi* x *B. tyrannus*

4b. Lateral spots usually present, usually distributed only below the level of the shoulder spot. Lateral scale rows usually 42-54. Predorsal scales usually 34-43. Gulf coast of Florida including Florida Bay.

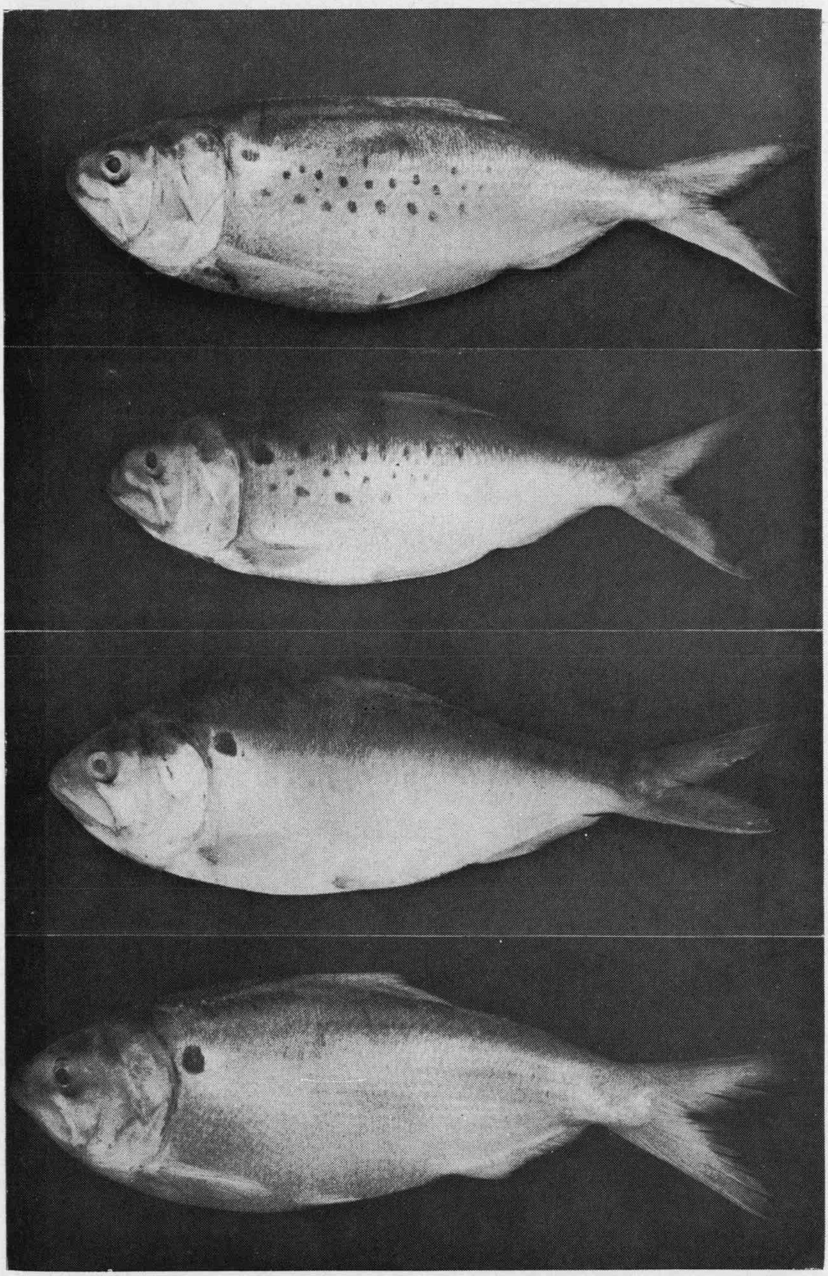
Hybrid *B. smithi* x *B. patronus*

Systematic Accounts

Genus *Brevoortia* Gill 1861

Brevoortia Gill, Proc. Acad. Nat. Sci., Philad., 1861: 37.

Characters.—Body oblong, compressed. Bony scutes number 27-34 on the median line of chest and abdomen, producing a sharp edge. Scales adherent, the exposed part much deeper than long, the margin serrate or pectinate in adults. Two series of modified scales present next to median line on back in front of dorsal fin, 28-56 scales in each series. Lateral scale rows between operculum and caudal fin base number 35-80. Cheek deeper than long. Mouth large. Maxillary extending to or beyond middle of eye. Upper jaw with a distinct median notch. Lower jaw included in upper jaw. Teeth absent in adults. Gill rakers long and numerous, about 115-165 in adults, increasing in number with age, those on upper limb of first arch extending downward and over those on lower limb. Dorsal with 14-19 principal rays (13-18 branched rays), the last one not greatly produced. Anal with 17-23 principal rays (16-22 branched rays), the last one little enlarged. Pelvic fin small, with 7 rays. Pectoral fin with 14-18 rays. Opercle with 0-33 striations. Vertebral count, including hypural, 42-50. Intestine very long. Peritoneum black.



DISTRIBUTION.—Atlantic and Gulf of Mexico coasts of the United States, north to Nova Scotia and south to the Gulf of Campeche; Atlantic coast of southern Brazil south to Argentina.

Brevoortia tyrannus (Latrobe)—Atlantic Menhaden

FIGURE 1

Clupea tyrannus Latrobe 1802: 77 (drawing; type locality Chesapeake Bay).

Clupea menhaden Mitchell 1815: 21 (orig. descr.).

Clupea neglecta Rafinesque 1818: 206 (orig. descr., New York).

Alosa menhaden DeKay 1842: 259 (descr., New York).

Alosa sadina DeKay (not of Mitchell) 1842: 263 (descr., figure of *B. tyrannus*).

Clupea carolinensis Gronow 1854: 140 (orig. descr., type locality S. Carolina).

Brevoortia menhaden Gill 1873: 811 (utility and range).

Brevoortia tyrannus Goode 1878: 30-42 (orig. descr. variety *brevicaudata* and *B. patronus*, revision of menhaden).

Brevoortia tyrannus brevicaudata Goode 1879: 22 (natural and economic history).

Brevoortia brevicaudata Hildebrand 1948: 10 (synon., descr., range).

Brevoortia brevicaudata Hildebrand 1963: 363-365 (synon., descr.).

Brevoortia tyrannus Berry 1964: 726 (nominal *brevicaudata* recognized as malformed *B. tyrannus*).

REFERENCES SINCE 1960.—June 1961a: 1-13 (economic and natural history of *tyrannus* and *patronus*); June 1961b: 39 pp. (age and size of *tyrannus* in Atlantic fishery, 1957); Reintjes 1961: 7 pp. (eggs and larvae from *T. N. Gill* crusises); Monod 1961: 506-547 (morphological comparison of *tyrannus* and *Ethmalosa fimbriata*); Reintjes and June 1961: 62-66 (commercial clupeids of Gulf of Mexico); Schwartz 1961: 384-408 (occurrence of juvenile *tyrannus* in June and July in Virginia and Maryland); Grant 1962: 45-47 (predation of bluefish on menhaden); Massmann *et al.* 1962: 42-45 (*tyrannus* larvae in Virginia); Hildebrand 1963: 257-454 (systematics, natural and economic history of *Brevoortia*

FIGURE 1. From top to bottom:

Brevoortia tyrannus. Adult 206 mm in standard length from Indian River at Sebastian, Indian River County, Florida, 1 Feb. 1965 (TU 37148). Long-headed form typical of northern specimens.

B. tyrannus. Adult 182 mm in standard length from Indian River at Eau Gallie, Brevard County, Florida (TU 37788). Short-headed form found commonly in the Indian River.

Hybrid *B. smithi* x *tyrannus*. Adult 197 mm in standard length from Indian River at Sebastian, Indian River County, Florida (TU 39974).

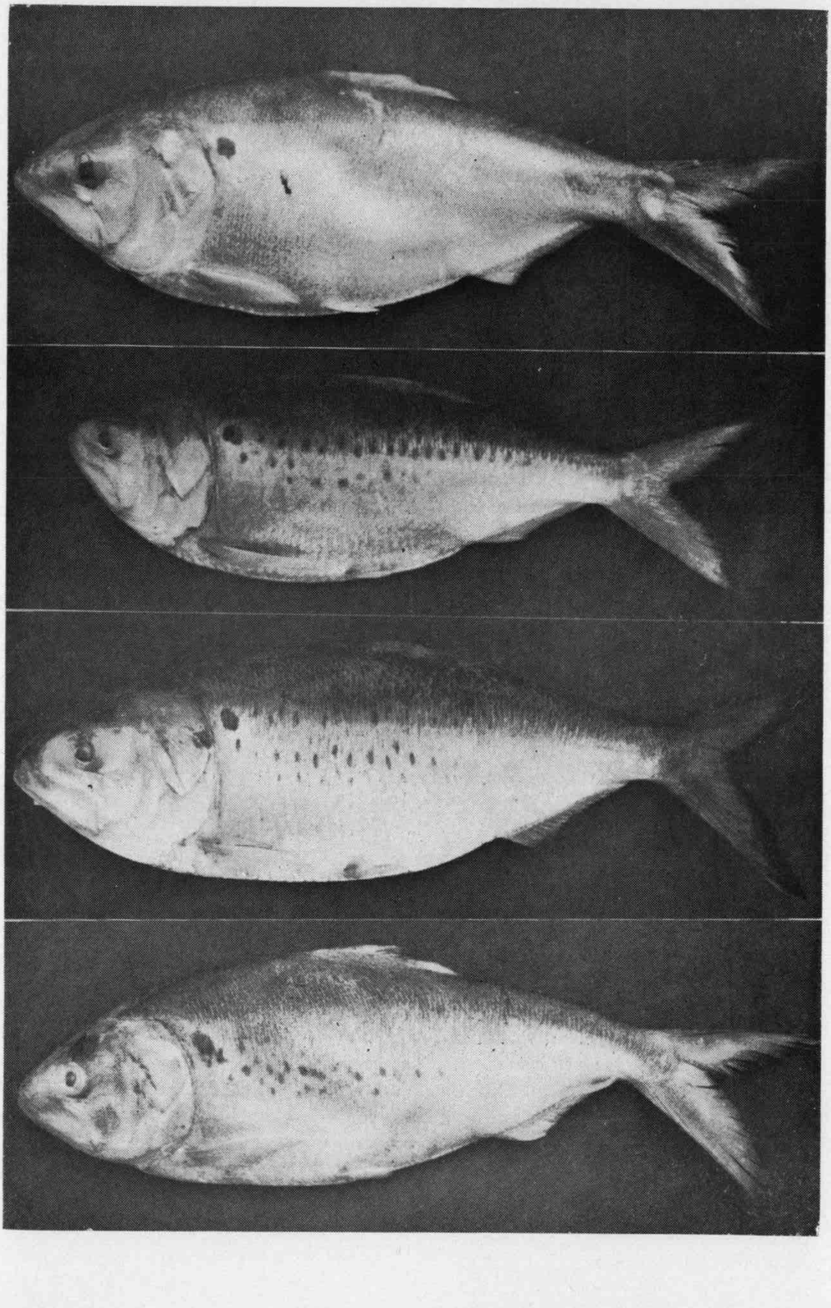
B. smithi. Adult 209 mm in standard length from Indian River at Sebastian, Indian River County, Florida, 15 May 1965 (TU 37719).

spp.); Roithmayr 1963: 22 pp. (distribution of purse seine sets for Atlantic menhaden, 1955-1959); Sutherland 1963: 1-21 (two subpopulations of *tyrannus* determined from vertebral counts); Reintjes 1964a: 108-113 (Florida fisheries for *tyrannus, patronus, smithi*); Reintjes 1964b: 531-549 (bibliography on *Brevoortia, Ethmalosa, Ethmidium*); Berry 1964: 720-730 (review and emendation to: Family Clupeidae [In] Fishes of Western North Atlantic); June and Nicholson 1964: 40 pp. (age and size of *tyrannus* in Atlantic fishery, 1958); Higham and Nicholson 1964: 255-271 (season and age of spawning by *tyrannus*); Anderson and Gehringer 1965: 79 pp. (*Brevoortia* sp. caught but not commercially important in Cape Canaveral area); Christensen 1965 (*tyrannus* and *smithi* in Loxahatchee River in Florida, southernmost record from Atlantic Ocean); Cooper 1965; 412 (large *tyrannus* from Rhode Island); June 1965: 12 pp. (spring and fall spawning populations of *tyrannus* with different vertebral counts); Pacheco and Grant 1965: 32 pp. (seasonal occurrence of juvenile *tyrannus* in Delaware); Lewis 1965: 409-412 (temperature effect on larval *tyrannus*); Henry 1966: 39 pp. (annual report of Menhaden Program); Nicholson and Higham 1965: 24 pp. (age and size of *tyrannus* in Atlantic fishery, 1962); Reintjes and Pacheco 1966: 50-58 (the relation of menhadens to estuaries); Henry 1967: 30 pp. (annual report of Menhaden Program); Dahlberg 1969a: 111-115 (parasitic isopod and copepod on menhadens from Florida); Dahlberg 1969b: 117-126 (fat cycles of menhadens from Florida).

MATERIAL.—Massachusetts: Provincetown, Sept. 1879, USNM 23773, 24424 (2, 217-270); Woods Hole, 2 Sept. 1871, USNM 10405 (3, 234-262); Woods Hole, 12 Sept. 1892, USNM 77794 (18, 98.4-147); Mass. Bay, USNM 26706 (2, 228-244); Mass. Bay, 2 July 1965, TU 37767 (1, 246); Barnstable Co., Childs River, 2 Sept. 1964, TU 40407 (12, 54.6-91.9). New York: Long Island, Greenport, 18 May 1964, TU 39795 (3, 301-310). New Jersey: lower New York Bay, 5 July 1965, TU 37774 (89, 201-284). Chesapeake Bay: near Reedville, Va., 6 July 1965, TU 37780 (145, 168-282). North Carolina: lower Newport River, 9 July 1965, TU 37779 (108, 165-188). Florida: off Jacksonville Beach, 14 May 1965, TU 37716 (92, 154-188); Indian River at Sebastian, 15 May 1965, TU 37717 (27, 165-236); Indian River at Sebastian, 1 Feb. 1965, TU 37148 (52, 148-325); Indian River at Sebastian, 19 Feb. 1965, TU 37162 (10, 207-260); Jupiter Inlet, 27 Dec. 1964, FSU 12435 (2, 200-221).

DESCRIPTION.—A species of *Brevoortia* characterized by vertebrae 46-48 (44-49), total predorsal scales 35-44 (33-46), ventral scutes 31-34 (29-34), lateral scale rows 43-53 (40-58), outer row of gill filaments on ceratobranchial arch 53-64 (51-66). Gill filaments increase from a mean of 52.0 in specimens 89.4 mm mean S.L. to 57.9 at 242.0 mm mean S.L. Branched dorsal rays 16-17 (15-18), branched anal rays 18-20 (16-21), pectoral rays 15-17 (14-18), opercular striations 14-27 (12-33), gill rakers 120-160. Pseudobranchiae 26-38, increase from mean of 29 (range 26-32) in specimens 135 mm S.L. to 34 (28-38) at 220 mm. Ventral fin with inner rays, or at least middle rays, as long as or longer than outer rays, with a few exceptions north of North Carolina. Frontal groove well developed. Anal fin with melanin. Scale pectinations pointed. Body depth 32.6-34.8 (29.9-39.7), head depth 26.8-27.4 (24.6-29.7), head length 30.8-32.4 (28.8-34.3), caudal peduncle depth 8.9-9.4 (8.2-10.1) pectoral fin length 17.9-19.2 (16.9-20.8), anal fin base length 15.2-16.6 (13.5-18.5), dorsal fin base length 19.3-20.2 (17.3-22.3), mandible length 16.7-17.9 (15.0-19.0), upper jaw length 14.3-15.2 (12.7-16.0).

COMPARISON.—*B. tyrannus* is markedly different from the other



large-scaled menhaden, *patronus*, in having a greater number of gill filaments on the ceratobranchial arch, vertebrae, predorsal scales and ventral scutes. *B. tyrannus* can be separated from the other Atlantic species, *smithi*, by the shape of the scale pectinations and ventral fin; the presence of a frontal groove, lateral spots, copious body mucus, softer flesh, and larger scales; more vertebrae, gill filaments, and opercular striations; fewer predorsal scales and lateral scale rows; more xanthin and melanin on the body and anal fin.

RANGE.—Hildebrand (1963) gives the range as Nova Scotia to Indian River City, Florida. This species is common in the Indian River, Florida, gill-net fishery. A recent collection, made available by Robert F. Christensen from the Loxahatchee River in the area of Jupiter Inlet, represents the southernmost record of its range in the Atlantic Ocean.

SIZE.—*B. tyrannus* is the largest menhaden and reaches a maximum total length of about 500 mm (Hildebrand, 1963). The largest authenticated specimen was 470 mm total length (tips of caudal fin lacking), 418 mm fork length and 380 mm standard length (Cooper, 1965). In the 1961 commercial fisheries *tyrannus* averaged about 180 mm fork length in the southern Atlantic and about 280 mm in the northern Atlantic (Nicholson and Higham, 1965). Although the south Atlantic fishery relies on smaller fish on the average, large specimens of *tyrannus* (up to 325 mm standard length) were caught with gill nets in the Indian River, Florida.

Brevoortia patronus Goode—Gulf Menhaden

FIGURE 2

Brevoortia patronus Goode 1878: 39 (orig. descr. based on this species and *B. gunteri* from Texas coast).

FIGURE 2. From top to bottom:
Brevoortia gunteri. Adult 222 mm in standard length from between Grand Bar and Empire Canal, Plaquemine Parish, Louisiana, 7 July 1964 (TU 40810).
B. patronus. Adult 186 mm in standard length from Carrabelle, Franklin County, Florida, 17 May 1965 (TU 37729). Average size of fish seen in commercial fisheries.
B. patronus. Adult 220 mm in standard length from Horseshoe Beach, Dixie County, Florida, 14 Nov. 1965 (TU 40174). A large specimen, found commonly on the gulf coast of peninsular Florida.
Hybrid *B. smithi* x *patronus*. Adult 236 mm in standard length from Sarasota Bay, Manatee County, Florida, 9 Nov. 1965 (TU 39774). Lower row of lateral spots is typical of gulf coast hybrid.

Brevoortia tyrannus patronus Evermann and Kendall 1894: 105 (Atlantic and gulf forms considered similar).

Brevoortia tyrannus Henshall (not of Latrobe) 1895: 211 (Tampa, Florida).

Brevoortia patronus Hildebrand 1948: 1-39 (review of the genus, descr. of *B. gunteri*).

REFERENCES SINCE 1960.—Darnell 1961: 553-568 (*patronus* in food chain); Gunter and Demoran 1961: 39-42 (cephalic lateral lines on *patronus*); June 1961a: 1-13 (economic and natural history of *patronus* and *tyrannus*); Reintjes and June 1961: 62-66 (fishery potential of *patronus*); Suttkus and Sundararaj 1961: 171-182 (fecundity and reproduction in *patronus*); Breuer 1962: 153-183 (*gunteri, patronus* in Lower Laguna Madre); Darnell 1962: 434-444 (*patronus* mentioned); Roithmayr and Waller 1963: 301-302 (seasonal movements of *patronus*); Gunter 1964: 99-108 (Gulf of Mexico menhaden fishery in relation to sports fisheries); Reintjes 1964a: 108-113 (Florida fisheries for *tyrannus, patronus, smithi*); Thompson 1966: 29-67 (fat cycle of *patronus*); Chapoton 1967: 60 (scale development in *patronus*); Hettler 1968: 119-123 (artificial hybrids of *smithi* and *patronus* and backcross with *smithi*).

MATERIAL.—Florida: Manatee Co., Sarasota Bay, 9 Nov. 1965, TU 39772 (8, 202-229); Pinellas Co., Tampa Bay (Boca Ciega Bay), 14 Feb. 1964, BCFSP uncat. (2, 195-213); Levy-Dixie Co., off mouth of Suwannee River, 1 Sept. 1965, TU 39789 (79, 185-215); Dixie Co., Horseshoe Beach, 14 Nov. 1965, TU 40174 (3, 220-232), 12 Dec. 1965, TU 39791 (11); Franklin Co., Carrabelle, 15 May 1965, TU 37731 (18, 185-212); Franklin Co., Carrabelle, 17 May 1965, TU 37729 (115, 166-207); Gulf Co., Port St. Joe, 9-14 July 1965, TU 37809 (15, 176-223). Louisiana: Lake Pontchartrain, 14 Sept. 1954, TU 9434 (6, 130-164); 30 Apr. 1958, TU 18605 (13, 148-183); 12 Nov. 1954, TU 9371 (12, 132-148); 5 Nov. 1954, TU 9415 (7, 135-159); Gulf of Mexico, 29° 10′ N., 89° 00′ W., 27 Feb. 1957, TU 17281 (2, 182); 29° 21′ N., 88° 55′ W., 30 Jan. 1958, RV Oregon 2093, TU 20038 (3, 166-173); 29° 22′ N., 88° 56′ W., 7 Mar. 1958, RV Oregon 2126, TU 17763 (87, 159-181); Bayou Geriov, Terrebonne Par., 13 June 1952, TU 4107 (1, 172); Whiskey Pass, Terrebonne Par., 15 May 1952, TU 1874 (3, 163-174); Redfield Bay, 29° 05′ N., 89° 05′ W., 4 Nov. 1957, TU 16882 (3, 135-200). Texas: Aransas Bay, 18-19 Aug. 1965, TU 38176 (76, 127-174).

DESCRIPTION.—A species of *Brevoortia* characterized by vertebrae 44-46 (43-47), total predorsal scales 29-37 (28-39), ventral scutes 29-31 (28-32), lateral scale rows 42-48, gill filaments on ceratobranchial arch 43-54 (41-56), branched dorsal rays 15-17 (14-17), branched anal rays 18-20 (17-21), pectoral rays 14-16 (14-17), opercular striations 13-27 (12-31), gill rakers 130-148, pseudobranchiae 24-36. Ventral fin with inner and middle rays usually as long as or longer than outer rays. Frontal groove well developed. Melanin on anal fin on Florida coast, but often lacking outside of Florida coast. Scale pectinations pointed. Body depth 37.2-39.4 (34.3-41.8), head depth 28.2-28.9 (26.9-30.3), head length 29.7-30.9 (28.2-32.8), caudal peduncle depth 9.0-9.4 (8.4-9.9), pectoral fin length 19.5-19.7 (18.3-21.3), anal fin base length 17.4-17.8 (15.6-20.0), dorsal fin base length 20.4-20.8 (18.4-23.3), mandible length 16.1-16.9 (14.9-18.3), upper jaw length 13.9-14.6 (13.1-15.5).

RANGE.—*B. patronus* probably ranges from Florida Bay along the gulf coast to the Gulf of Campeche, Mexico. Hildebrand (1963) gave the range as Tampa Bay, Florida to Texas. Christmas and Gunter (1960) reported young *patronus* from the Caloosahatchee River. Reintjes (1964a) reported adults from Naples and juveniles from Cape Sable before hybrids were known to exist. Hettler (1968) reported ripe *patronus* from near Naples and Sanibel Island. Although hybrid *smithi* x *patronus* occur south to Florida Bay, *patronus* is probably rare in Florida Bay. Hybrids may be maintained in the Florida Bay area by a southward movement along the Florida peninsula. Because the hybrids are all males they could not be a self-sustaining "hybrid population". In the western Gulf of Mexico, *patronus* ranges south to the Gulf of Campeche (Reintjes and June, 1961).

SIZE.—The largest specimen examined by Hildebrand (1963) was 207 mm standard length. Of 7,021 specimens measured by Christmas (unpub.) the longest was 225 mm fork length (214 mm S.L.). The largest *patronus* examined are from off Florida; standard lengths are 223 mm (Port St. Joe), 232 mm (Horseshoe Beach), and 229 mm (Sarasota Bay).

Brevoortia smithi Hildebrand—Yellowfin Menhaden

FIGURE 1

Brevoortia aureus Hildebrand (not of Agassiz) 1919: 7 (orig. descr. of *B. smithi* Hildebrand 1941; compared to *B. tyrannus*).

Brevoortia smithi Hildebrand 1941: 244 (*B. aureus* Hildebrand recognized as a distinct species without a name; *B. smithi* proposed; type locality Beaufort, N. C.).

REFERENCES SINCE 1948.—Caldwell 1954: 182-184 (misidentified *smithi* from Florida gulf coast as *gunteri*); Suttkus 1958: 401-410 (distribution of *Brevoortia* in Gulf of Mexico; comparison of *smithi* in Gulf of Mexico to *smithi* in Atlantic Ocean and to *gunteri*); Christmas and Gunter 1960: 338-343 (distribution of *Brevoortia* species in Gulf of Mexico; morphological comparison of *smithi* and *gunteri* from Mississippi River Delta area); Springer 1960: 17 pp. (*tyrannus* and *smithi* from St. Lucie and Indian River, Fla.); Springer and Woodburn 1960: 16-20 (ecological notes on *patronus* and *smithi* from Tampa Bay; samples of *patronus* probably included hybrids); Tabb and Manning 1961: 552-649 (*smithi* recorded from Florida Bay); Moody 1961: 1-18 (*smithi* in St. Johns River, Fla.); Reintjes 1962: 93-102 (eggs and larvae of *smithi*); Tabb and Manning 1962: 39-79 (Florida Bay record of *smithi* and *B. sp.*); Reintjes 1964a: 108-113 (Florida fisheries for *tyrannus, patronus, smithi*); Hettler 1968: 119-123 (artificial hybrids of *patronus* and *smithi* and backcross with *smithi*).

MATERIAL.—North Carolina: Beaufort; (no date given) USNM 144301 (7, 226-262); 5 Aug. 1915, USNM 125950 (1, 230); 5 Aug. 1915, USNM 125939 (1, 234); 3 Aug. 1915, USNM 125955 (1, 245); 6 Aug. 1915, USNM 125953 (1, 242); 5 June 1915, USNM 125947 (1, 247). Georgia: McIntosh Co., Sapelo Island, 29 Oct 1963, UG 828 (22, about 95). Florida: Putnam Co., St. Johns River, 6 Mar. 1964, TU 37740 (1 adult); St. Lucie Co., Fort Pierce, 25 Jan. 1965, uncat. (2, 211-228); Brevard Co., Eau Gallie, 17 Feb. 1965, TU 37160 (11, 194-234); Brevard Co., Eau Gallie, 17 Feb.-9 Mar. 1964, TU 39768 (16, 159-243); Indian River Co., Sebastian, 26 Feb. 1965, TU 37150 (22, 254-287), Palm Beach Co., Jupiter, Oct. 1965, TU 39793 (3, 254-256); Palm Beach Co., Loxahatchee River, 27 Nov. 1964, FSU 12343 (1, 182), 24 Aug. 1964, FSU 12103 (2, 180-187); Monroe Co., Florida Bay, 30 Oct. 1963, TU 39626, 39628, 39630 (84, 83-141); Collier Co., Naples, 16 May 1965, TU 37728 (120 juveniles); Charlotte Co., Charlotte Harbor, 15 Nov. 1965, TU 39788 (42, 191-252), Mar. 1966, TU 40959 (7 adults), 21 May 1964, BCFSP uncat. (17 juveniles); Manatee Co., Sarasota Bay, 9 Nov. 1965, TU 39773 (34, 203-243); Pinellas Co., Tampa Bay, BCFSP uncat., 22 Nov. 1963 (31, 143-239), 14 Feb. 1964 (8, 165-213), 24 Oct. 1963 (12, 124-154), 11 Apr. 1962 (1, 213), 16 Oct. 1962 (2, 142-158), 25 Oct. 1963 (4, 146-158), 6 May 1963 (4, 35-39), 24 Oct. 1963 (11, 84-113); Dixie-Taylor Co., mouth of Steinhatchee River, 1 Sept. 1965, TU 39786 (90, 213-268); Dixie Co., Horseshoe Beach, 14 Nov. 1965, TU 39764 (8 adults), 12 Dec. 1965, TU 39790 (3 adults); Franklin Co., Carrabelle, 15 May 1965, TU 37732 (25, 180-233); Gulf Co., Port St. Joe, 9-14 July 1965, TU 37808 (53, 192-269). Alabama: E. Dauphin (probably near Dauphin Island), Oct. 1959, GCRL uncat. (2, 218-229).

Description.—A species of *Brevoortia* characterized by vertebrae 44-45 (43-46), total predorsal scales 39-51 (37-56), ventral scutes 30-32 (29-34), lateral scale rows 57-73 (54-80), gill filaments on ceratobranchial arch 37-50 (35-52), branched dorsal rays 14-16 (13-17), branched anal rays 18-20 (16-22), pectoral rays 14-16 (14-17), opercular striations 2-11 (0-15), gill rakers 130-165 (Atlantic Ocean), 115-150 (Gulf of Mexico), pseudobranchiae 23-38. Scales between tip of pectoral fin and base of pelvic fin 3-5. Ventral fin with inner rays about one-half to two-thirds length of outer rays. Frontal groove absent. Melanin on anal fin absent or sparse but often moderate on the gulf coast of Florida. Body depth 37.1-38.9 (32.8-42.4), head depth 26.8-28.0 (25.3-29.1), head length 28.7-29.8 (27.6-31.0), caudal peduncle depth 9.7-10.2 (9.0-11.2), pectoral fin length 18.9-19.7 (17.1-22.1), anal fin base length 18.3-20.5 (15.7-21.5), dorsal fin base length 18.7-19.5 (16.8-21.9), mandible length 15.7-16.8 (14.8-17.5), upper jaw length 13.1-13.9 (11.9-14.7).

Comparison.—*B. smithi* is closely related to but distinguished from *gunteri* in having higher numbers of vertebrae and scutes, and a smaller head. The head depth and lengths of head, mandible and maxillary are greater in *gunteri*. *B. smithi* can readily be distinguished from large-scaled menhadens (*tyrannus* and *patronus*) by many characters (Tables 1, 2), including frontal groove, ventral fin shape, scale pectinations, lateral spots, body mucus, firmness of flesh, scale size, ovarian color, anal fin darkness, higher counts including predorsal scales and lateral scales, and lower counts including gill filaments, opercular striations and vertebrae (in Atlantic Ocean).

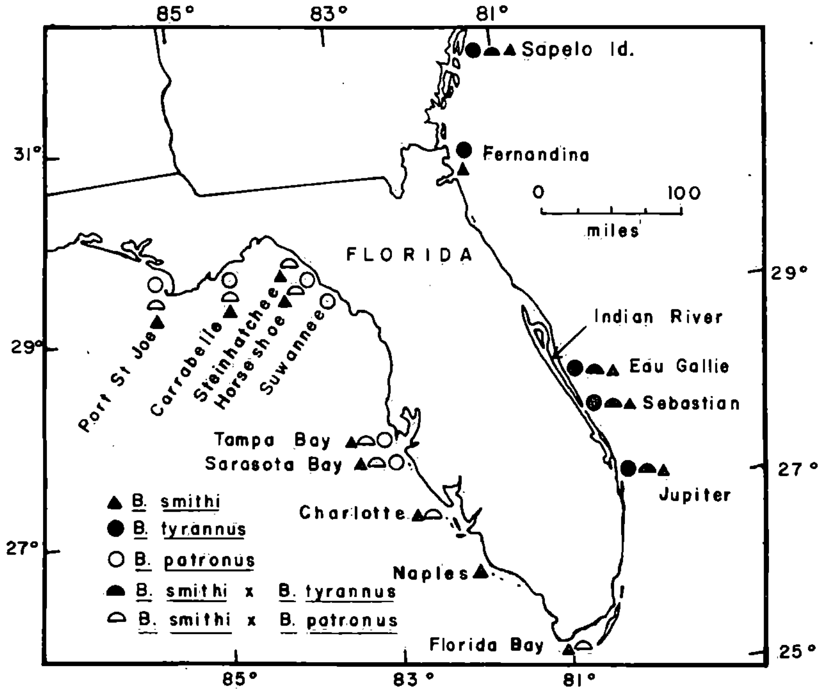


FIGURE 3. Distribution of *Brevoortia* samples from the Georgia and Florida region of the Atlantic and Gulf of Mexico.

RANGE. (Figure 3).—*B. smithi* has been recorded north to North Carolina and west to Louisiana, except for a complete or nearly complete separation on the Florida coast between West Palm Beach and Miami. Hildebrand (1948) gave the distribution as Beaufort, N. C. to "the Indian River, presumably Indian River City, Fla." Two recent collections from south of the Indian River at Jupiter Inlet and Loxahatchee River represent the southernmost records of the Atlantic population. The North Carolina specimens apparently represent the northern fringe of the Atlantic population because this species apparently moved that far north only in the spring and summer (Hildebrand, 1963), was present in such small numbers that it appeared to be nonschooling (Hildebrand, 1963), and has not been collected in North Carolina in recent years. Specimens were collected off Georgia in 1963 by Dr. D. C. Scott. The apparent decline of the Atlantic population could have resulted from commercial fishing or hybridization with the abundant *tyrannus*.

Caldwell's (1954) record of *gunteri* from Cedar Key on the Florida gulf coast was based on a specimen of *smithi* (Suttkus, 1958). Hildebrand (1963) noted that specimens from the west coast of Florida "are nearer to *smithi* than to *gunteri*". Christmas and Gunter (1960) gave the range in the gulf as Caloosahatchee River, Florida, to Chandeleur Sound, Louisiana. *B. smithi* was reported from Florida Bay first by Reintjes and June (1961) and most recently by Reintjes (1966), based on collections of the University of Miami Institute of Marine Science. Reintjes (1960) noted that *smithi* is most abundant from Cape Kennedy to St. Lucie Inlet on the Atlantic coast and from Cape Sable to Sarasota on the gulf coast of Florida. My collections show *smithi* to be common in the gulf from Florida Bay to the Florida panhandle. Although two specimens collected near Miami were identified as *smithi* (Frederick Berry, pers. comm.), the species apparently is rare on the Florida coast between West Palm Beach and Miami.

SIZE.—The largest specimen observed by Hildebrand (1963) was a 330-mm specimen (274 mm standard length) from North Carolina. A specimen from the Indian River on the east coast of Florida was 287 mm standard length. The largest specimen from the west coast of Florida, taken at Port St. Joe, was 269 mm.

Brevoortia gunteri Hildebrand—Gulf Finescale Menhaden

FIGURE 2

Brevoortia patronus Goode (in part *B. gunteri* Hildebrand) 1879: 39 (diagn., tables based in part on *B. gunteri*).

Brevoortia sp. Gunter 1945: 27 (unnamed species in gulf).

Brevoortia gunteri Hildebrand 1948: 31 (orig. descr.; type locality Aransas Bay, Texas).

REFERENCES SINCE 1948.—Gunter 1950: 89-101 (*gunteri* common on Texas coast February to June); Miles and Simmons 1950: 1-28 (gulf menhaden fishery; *patronus, gunteri*); Hildebrand 1954: 169-232 (*gunteri* from Gulf of Campeche); Simmons 1957: 156-200 (*patronus* and *gunteri* in Upper Laguna Madre); Hoese 1958: 312-352 (*gunteri* and *patronus* listed); Suttkus 1958: 401-410 (distribution of *Brevoortia* in Gulf of Mexico; comparison of *smithi* in gulf to *smithi* in Atlantic and to *gunteri*); Robertson 1959: (osteology of *patronus* and *gunteri*); Christmas and Gunter 1960: 338-343 (distribution of *Brevoortia* species in Gulf of Mexico; morphological comparison of *smithi* and *gunteri* from Mississippi River Delta area); Breuer 1962: 153-183 (*gunteri* and *patronus* in Lower Laguna Madre).

MATERIAL.—Louisiana: between Grand Isle, Louisiana and Dauphin Island, Alabama, 23 July 1962, TU 28174 (1, 253); Plaquemine Par., 7 July 1964, TU 40810 (1, 222); Terrebonne Par., Timbalier Island, GCRL uncat., 28 July

1960 (5, 222-248), 5 Aug. 1960 (8, 213-251); Jefferson Par., Grand Isle, GCRL uncat., 2 June 1960 (1, 235), 3 June 1960 (3, 225-252); Terrebonne Par., Wine Island Pass, GCRL uncat., 21 July 1960 (4, 216-231); Cameron Par., Sabine, GCRL uncat., 17 Aug. 1960 (1, 241); Plaquemine Par., west of West Bay, GCRL uncat., 27 June 1961 (2, 226-233); 29° 31′-29° 35′ N., 92° 45′-92° 54′ W., GCRL uncat., 6 Aug. 1960, RV *Oregon* 2869 (2, 216-226). Texas: Galveston Co., Galveston Beach, GCRL uncat., 3 Oct. 1957 (2, 210-212), 3 May 1957 (2, 221-222); 28° 39′ N., 95° 50′ W., 13 Aug. 1960, GCRL uncat., RV *Oregon* 2903 (11, 162-214); Aransas Co., St. Joseph Island, 14 July 1948, TAMU E-1-a-7 (11, 142-213); 28° 14′ N., 96° 34′ W., 15 Aug. 1960, RV *Oregon* 2914, GCRL uncat., (4, 165-204). Mexico: 5 K. south of Veracruz, 20-21 Jan. 1958, UF no. F-5719 (1, 117); Cuidad del Carmen, 8 June 1960, USNM 179892 (2, 204-210); Campeche to Chompoton, 10-16 Feb. 1951, TIMS uncat. (2, 163-170).

Description.—A species of *Brevoortia* characterized by vertebrae 42-43 (41-43), total predorsal scales 40-49 (39-52), ventral scutes 28-30 (27-31), lateral scale rows 65-72 (60-76), gill filaments on ceratobranchial arch 40-49 (38-52), branched dorsal rays 14-15 (13-16), branched anal rays 19-22 (18-22), pectoral rays 15-16 (14-17), opercular striations 5-12 (0-18), gill rakers 140-160 (Figure 8) pseudobranchiae 25-35. Scale rows between tip of pectoral fin and base of ventral fin 1 or 2. Ventral fin with inner rays one-half to two-thirds length of outer rays. Frontal groove absent. Scale pectinations rounded. Body depth 38.9-39.2 (34.7-41.6), head depth 29.5-30.5 (28.0-32.0), head length 31.4-32.3 (29.8-33.3), caudal peduncle depth 10.1-10.5 (9.1-11.2), pectoral fin length 20.5-20.6 (18.7-23.3), anal fin base length 20.5-20.8 (18.9-23.2), dorsal fin base length 19.0-19.4 (16.9-22.1), mandible length 18.7-18.9 (17.3-20.6), upper jaw length 15.5-16.0 (14.5-16.9).

Range.—The known range of *gunteri* is from Chandeleur Sound, Louisiana, to the Gulf of Campeche. Hildebrand (1948, 1963) gave the range as Grand Isle, Louisiana, to the mouth of the Rio Grande River. Christmas and Gunter (1960) extended the known range east to Chandeleur Sound, Louisiana, and south to the Gulf of Campeche. Reintjes (1960) noted: "there is evidence to suggest that it extends around the Yucatan Peninsula and into the Caribbean Sea."

Size.—The largest specimen recorded, 264 mm standard length, was collected off Louisiana (Christmas and Gunter, 1960).

Hybrid *Brevoortia smithi* x *B. tyrannus*

Atlantic Hybrid Menhaden

Figure 1

Brevoortia sp. Reintjes 1960: 33 (reference to an unidentifiable form of menhaden on central Atlantic coast of Florida); Reintjes 1966: 16 (electrophoretic pattern of fish believed to be hybrid *smithi* x *tyrannus* was same as *smithi* pattern).

Material.—Georgia: McIntosh Co., Sapelo Island, 20 Oct. 1963, UG 828 (2, 95). Florida: Brevard Co., Eau Gallie, 1 Feb. 1965, TU 37143 (32, 165-232), 27 Feb. 1965, TU 37156 (12, 200-246); Indian River Co., Sebastian, 14 July

1965, TU 37791 (19, 203-248), 1 Feb. 1965, TU 37146 (3, 199-204), 14 Dec. 1965, TU 39783 (19, 190-229); Palm Beach Co., Jupiter Inlet, Oct. 1965, TU 39371 (2, 252-253), Loxahatchee River, 27 Dec. 1964, FSU 12435 (1, 244).

DESCRIPTION.—A hybrid form of *Brevoortia* characterized by vertebrae 44-46, total predosal scales 38-46 (36-49), ventral scutes 31-33 (29-34), lateral scale rows 44-59 (42-63), gill filaments on ceratobranchial arch 42-50 (40-55), branched dorsal rays 15-16 (15-17), branched anal rays 18-21 (17-22), pectoral rays 15-16 (14-17), opercular striations 10-20 (10-23), pseudobranchiae 22-33. Ventral fin usually with both middle and inner rays slightly shorter than outer rays (87% of specimens). Frontal groove usually shorter than in *tyrannus* (59% of specimens) but may be absent or well developed. Anal fin dusky. Scale pectinations usually pointed. Body depth 35.1-36.9 (33.7-39.6), head depth 26.3-27.3 (25.3-29.2), head length 28.7-29.4 (28.0-31.4), caudal peduncle depth 9.0-9.6 (8.8-10.7), pectoral fin length 19.1-19.7 (17.1-21.7), anal fin base length 18.2-18.7 (17.8-19.8), dorsal fin base length 19.6-19.8 (17.7-21.4), mandible length 15.7 (14.7-17.2), upper jaw length 13.3-13.4 (12.3-14.7).

COMPARISON.—Hybrids from both Atlantic (*smithi* x *tyrannus*) and gulf (*smithi* x *patronus*) coasts of Florida can be separated with confidence from the corresponding large-scaled menhadens by a combination of characters (Tables 1 and 2) including the frontal groove, ventral fin shape, lateral spots, number and appearance of opercular striations, and certain meristic characters (especially predorsal scales in Gulf of Mexico, vertebrae in Atlantic Ocean, gill filaments, and opercular striations). Both hybrid forms can be separated from *smithi* by a combination of characters including frontal groove, ventral fin shape, scale size, scale pectinations, lateral spots (valuable for Gulf of Mexico specimens), quantity of mucus (fresh specimens), firmness of flesh (fresh specimens), numbers and appearance of opercular striations, and certain meristic characters (predorsal scales, lateral scale rows).

RANGE. (Fig. 3).—Hybrids have been collected south to Jupiter Inlet and north to Sapelo Island, Georgia. They are abundant in the Indian River gill net fishery.

SIZE.—The largest hybrids from the Atlantic coast of Florida are 253 (Jupiter Inlet) and 248 mm standard length (Indian River).

Hybrid *Brevoortia smithi* x *B. patronus*

Gulf Hybrid Menhaden

FIGURE 2

Brevoortia patronus Springer and Woodburn 1960: 16-20 (*patronus* samples studied from Tampa Bay; hybrid *smithi* x *patronus* I expect were probably included in *patronus* samples).

Table 1. COMPARISON OF *Brevoortia* SPECIES AND HYBRID FROM INDIAN RIVER, FLORIDA

Character	*B. tyrannus*	Hybrid	*B. smithi*
Frontal groove	Complete	Usually reduced in length	Absent
Ventral fin	Inner rays, or at least middle rays, equal in length to outer rays	Fin intermediate, usually with both inner and middle rays slightly less than outer rays	Inner rays about one-half to two-thirds length of fin
Scale pectinations	Pointed, length medium or long	Usually pointed, medium length	Rounded tip, shorter
Lateral spots	Usually present above and below level of shoulder spot	Usually absent but sometimes with lower row	Absent
Body mucus	Copious	Copious	Sparse
Firmness of flesh	Soft	Soft	Firm
Total predorsal scales	Usually 35-44 (34-46)	Usually 36-47 (36-49)	Usually 44-53 (40-56)
Vertebrae	Usually 46-47 (44-48)	44-46	44-46
Lateral scale rows	Usually 43-49 (42-52)	Usually 44-61 (42-63)	64-75
Gill filaments	53-65	Usually 40-51 (40-55)	Usually 41-52 (39-52)
Opercular striations	Usually 14-27 (12-31)	Usually 10-20 (10-23)	Usually 3-10 (0-12)
Anal fin darkness	Moderate or black appearance	Very little or moderate	Very little or no melanin
Ovarian color	Yellow		White
Scale size	Large	Large	Small

Table 2. COMPARISON OF *Brevoortia* SPECIES AND HYBRID FROM THE FLORIDA GULF COAST

Character	*B. patronus*	Hybrid	*B. smithi*
Frontal groove	Complete	Usually reduced in length	Absent
Ventral fin	Inner rays equal or longer than outer rays	Fin intermediate, usually with both inner and middle rays slightly less than outer rays	Inner rays about one-half to two-thirds length of fin
Scale pectinations	Pointed	Usually pointed	Rounded tip, short
Lateral spots	Usually present above and below level of shoulder spot	Usually present below level of shoulder spot	Absent, rarely with lower row present
Firmness of flesh	Soft	Soft	Firm
Total predorsal scales	Usually 29-37 (28-39)	Usually 34-42 (32-43)	Usually 39-49 (37-54)
Vertebrae	Usually 44-46	44-46	Usually 44-45 (43-45)
Lateral scale rows	42-48	Usually 43-52 (42-55)	Usually 55-71 (54-76)
Gill filaments	Usually 44-54 (42-56)	Usually 39-47 (38-48)	Usually 38-48 (35-50)
Opercular striations	Usually 13-25 (12-31)	Usually 10-21 (9-24)	Usually 0-11 (0-15)
Anal fin darkness	Very little, moderate or black appearance	Varies with locality	Little or none, sometimes moderate
Scale size	Large	Large	Small

Brevoortia sp. Tabb and Manning 1962: 61 (Florida Bay records of *smithi* and unidentifiable adults; the latter are probably hybrids).

Brevoortia hybrid (*smithi* x *patronus*) Turner 1967: 20-22 (collections off southwestern Florida included *smithi*, *patronus*, and intermediate specimens; artificial crosses of *smithi* with *patronus*, and *smithi* with intermediate form); Hettler 1968: 119-123 (artificial hybrids of *smithi* and *patronus* and backcross with *smithi*).

MATERIAL.—Florida: Monroe Co., Florida Bay, 30 Oct. 1963, TU 39627, 39629, 39631 (15, 92-139); Charlotte Co., Charlotte Harbor, 15 Nov. 1965, TU 39787 (3, 208-243), Mar. 1966, TU 40958 (42 adults), 21 May 1964, BCFSP uncat. (18, 65-83); Manatee Co., Sarasota Bay, 9 Nov. 1965, TU 39774 (68, 187-245); Pinellas Co., Boca Ciega Bay (Tampa Bay), 14 Feb. 1964, BCFSP uncat. (4, 188-198), 22 Nov. 1963, BCFSP uncat. (2, 195-203); Dixie Co., Horseshoe Beach, 14 Nov. 1965, TU 39765 (7 adults), 12 Dec. 1965, TU 39792 (4 adults); Dixie-Taylor Co., mouth of Steinhatchee River, 1 Sept. 1965, TU 39785 (56, 213-255); Franklin Co., Carrabelle, 15 May 1965, TU 39800 (5, 219-225); Gulf Co., Port St. Joe, 9-14 July 1965, TU 37810 (6, 216-243).

DESCRIPTION.—A hybrid form of *Brevoortia* characterized by vertebrae 45 (44-46), total predorsal scales 34-43 (32-43), ventral scutes 30-31 (29-32), lateral scale rows 43-50 (42-55), gill filaments on ceratobranchial arch 39-47 (38-48), branched dorsal rays 15-16 (14-17), branched anal rays 18-21 (17-22), pectoral rays 15-17 (14-18), opercular striations 10-19 (9-24). Ventral fin usually with both inner and middle rays slightly less than outer rays (83% of specimens). Frontal groove usually shorter than in *patronus* (71% of specimens). Darkness of anal fin variable. Scale pectinations usually pointed. Body depth 35.1-37.2 (32.2-39.6), head depth 26.7-27.0 (25.2-29.0), head length 28.7 (27.0-30.3), caudal peduncle depth 9.0-9.3 (8.6-10.2), pectoral fin length 19.1-19.6 (17.4-21.5), anal fin base length 18.2-18.6 (16.4-21.2), dorsal fin base length 19.5-20.0 (17.8-21.7), mandible length 15.5-15.8 (14.2-16.7), upper jaw length 13.1-13.4 (11.8-14.2).

RANGE. (Fig. 3).—This hybrid appears to be common along the gulf coast of Florida from Florida Bay to Port St. Joe. Large series of adults are from Charlotte Harbor, Sarasota Bay, and off the Steinhatchee River. Only juveniles are available from Florida Bay but a few unidentified adults (Tabb and Manning, 1962) probably are hybrids.

SIZE.—The largest hybrid from the gulf coast of Florida (255 mm standard length) is from the Steinhatchee River area.

CHARACTERISTICS OF HYBRIDS

(*B. smithi* x *B. tyrannus* and *B. smithi* x *B. patronus*)

To identify hybrids it was necessary to determine the range of variation of the parental species' characters. Specimens of *smithi* from its population fringes (Alabama and North Carolina), where hybridization is not known to occur, agreed with those from the

Florida coasts that were previously separated by eye using field characters. Most specimens were readily distinguishable as one of the parental species or hybrids because of their many differences. Some specimens that appeared to be backcrosses were included with the hybrids. Of the several hundred hybrids from both the Atlantic and gulf coasts for which the sex was determined, all were males except one. This distinct hybrid from Indian River, Florida, had a small ovary with immature oocytes. Variation of the parental species' characters can be determined by analyzing only females, but this approach was not used. Characters that separate *smithi* from hybrids correspond to the characters of the cognate *gunteri*. Hybrids were separated by "field characters" and analyses of counts, proportions, and sex ratios confirmed my identifications.

Some distinguishing characters are given in Table 1 for Atlantic forms and Table 2 for gulf forms.

Qualitative Morphological Characters

Frontal Groove (Fig. 4, Table 3).—The frontal groove is present in adult and larger juveniles of *tyrannus* and *patronus*, but can be obscured when damaged. This character is absent in *smithi* and *gunteri*; rarely they have a bowl-shaped depression in the anterior region, but this does not look like a frontal groove. This groove was induced in juvenile specimens of *smithi* and hybrids from Florida Bay that were left too long in a strong formalin solution. In both hybrid forms the frontal groove is usually present, but it may be absent or complete; it is reduced in length or discontinuous in 59% of the Atlantic hybrids and 71% of the gulf hybrids.

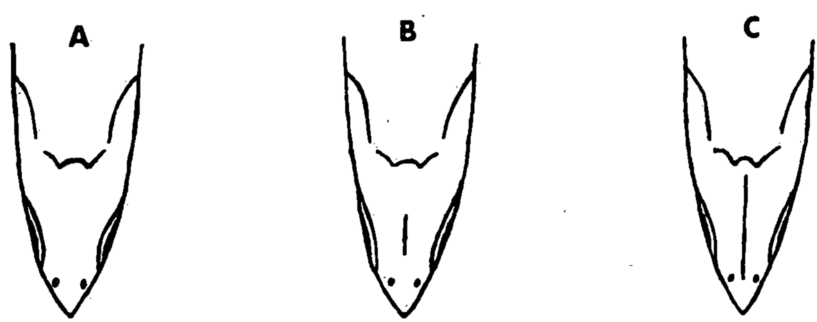


Figure 4. Frontal groove lengths in *Brevoortia*: A, absent; B, short or sometimes discontinuous; C, complete.

Table 3. FRONTAL GROOVE LENGTHS EXPRESSED IN PERCENTAGES

Locality	N	A[1]	B[1]	C[1]
Indian River				
B. tyrannus	46	0	0	100
Hybrid	38	21	61	18
B. smithi	46	100	0	0
Jupiter				
B. tyrannus	2	0	0	100
Hybrid	3	33	33	33
B. smithi	6	100	0	0
Sarasota				
B. patronus	10	0	0	100
Hybrid	53	6	60	34
B. smithi	47	100	0	0
Steinhatchee				
B. patronus	33	0	0	100
Hybrid	31	16	84	0
B. smithi	50	100	0	0
Apalachicola				
B. patronus	35	0	0	100
Hybrid	7	0	100	0
B. smithi	51	100	0	0

[1]Categories A, B, C as in Figure 4.

PELVIC FIN (Fig. 5, Table 4).—When folded, the inner rays or at least the middle rays of the pelvic fin, with few exceptions, are as long as the outer rays in *tyrannus* and *patronus*. In *smithi* and *gunteri* the inner rays are considerably shorter, about one-half to two-

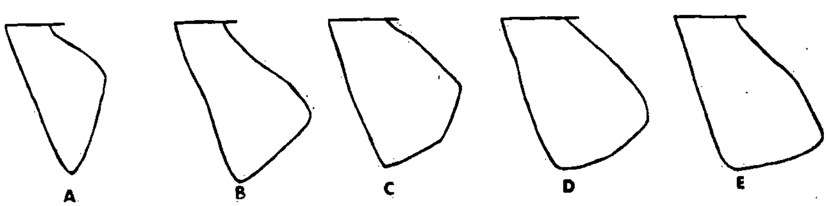


FIGURE 5. Pelvic fin shapes in *Brevoortia*: A, inner rays of ventral fin short, one-half to two-thirds length of fin; B, both inner and middle rays slightly shorter than outer rays; C, inner rays shorter than outer but middle rays as long or longer than outer rays; D, inner and outer rays of equal length; E, inner rays longer than outer rays.

Table 4. Pelvic Fin Shapes Expressed in Percentages

Locality	N	A[1]	B[1]	C[1]	D[1]	E[1]
B. tyrannus						
Massachusetts	35		14	77	6	3
New Jersey	29		3	69	28	
Chesapeake Bay	49		4	80	16	
North Carolina	27			96	4	
Fernandina	43			67	30	2
Indian River	55			47	51	2
Jupiter	2			100		
B. smithi × *tyrannus*						
Indian River	57	5	86	5	4	
Jupiter	3		100			
B. smithi						
North Carolina	12	100				
Indian River	45	100				
Jupiter	6	100				
Florida Bay	25	100				
Charlotte	30	100				
Sarasota	68	100				
Steinhatchee	50	98	2			
Apalachicola	52	96	4			
B. smithi × *patronus*						
Florida Bay	15	20	80			
Charlotte	12	42	58			
Sarasota	58	12	79	9		
Steinhatchee	47	2	94	4		
Apalachicola	8	13	88			
B. patronus						
Sarasota	10				20	80
Steinhatchee	48		2	8	56	33
Apalachicola	34			6	74	21
Louisiana	47			6	53	40
Texas	25			12	36	52
B. gunteri						
Louisiana	30	100				
Texas	30	93	7			
Mexico	5	100				

[1]Categories A—E as in Figure 5.

thirds the length of the outer rays. Both hybrid combinations are intermediate; both the inner and middle rays are slightly shorter than the outer rays in 87% of the Atlantic hybrids and in 83% of the gulf hybrids. In all forms when the innermost ray occasionally was greatly reduced, it was considered to be aberrant.

SCALE PECTINATIONS (Fig. 6).—Scale pectinations increase in length throughout life. Scale pectinations in adults of *tyrannus* and *patronus* are pointed but may be thin over most of their length, or conical with a wide base. Pectinations in *smithi* and *gunteri* have a blunt rounded tip; they are usually cylindrical but may be conical or with tip larger than base (club-shaped). Pectinations are relatively short in the small-scaled menhadens. In the hybrid the pectinations are long as in the large-scaled menhadens; they are usually thin or conical, rarely cylindrical or club-shaped. Different types are sometimes present on the same scale, especially in hybrids. Scale pectinations are twice normal length (Fig. 6C) in one *patronus* specimen from Sarasota Bay. This may result from a new gene combination as the specimen appears to be modified by introgressive hybridization.

MUCUS.—*B. tyrannus, patronus*, and both hybrids have copious body mucus. *B. smithi* and *gunteri* have little. Hildebrand (1963) states "*tyrannus* is slimy and slippery and *smithi* is not." Fresh *tyrannus* and Atlantic hybrids can be separated from *smithi* by feel.

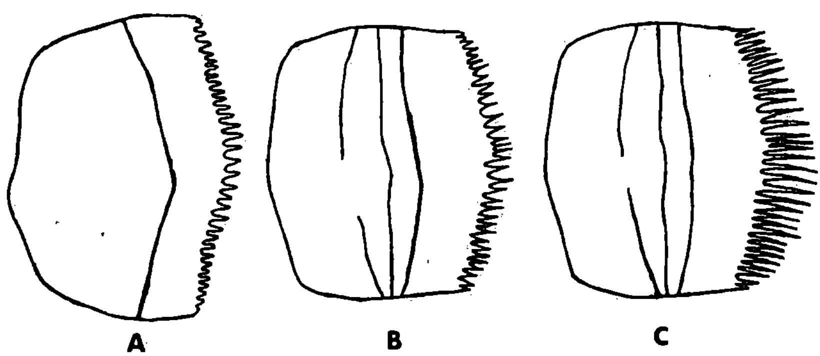


FIGURE 6. Schematic representations of scale types in adult *Brevoortia*, modified from Hildebrand (1963). All scales taken from middle of side below dorsal fin and about equally enlarged. A, scale type of small-scaled menhadens from *smithi* 295 mm total length. B, scale type of large-scaled menhadens and both hybrid combinations, from *patronus* 215 mm total length; this scale is larger than A in specimens of equal size; number of transverse grooves is variable. C, scale of only specimen seen with abnormally long scale pectinations, *patronus* 202 mm standard length.

FIRMNESS OF FLESH.—*B. tyrannus* and the Atlantic hybrid have soft flesh while that of *smithi* is firm.

TIME REQUIRED TO FREEZE.—When placed simultaneously in a freezer, *tyrannus* takes about twice as long to freeze solid as *smithi* does, and hybrids are somewhat intermediate.

COLOR PATTERNS

LATERAL SPOTS.—Series of lateral spots (except the shoulder spot, which is present in all species) are usually present in *tyrannus* at or above the level of the shoulder spot, and also below. They are absent in *smithi* and *gunteri*, except for two adult *smithi* from Sarasota and Steinhatchee that have a lower row; these are typical *smithi* in other characters. Hybrids from the Atlantic coast of Florida usually lack lateral spots, but occasionally have a lower row present. Hybrids from the gulf coast usually have only a lower row of spots present, but they may lack spots or have a full complement. Lateral spots appeared on specimens of species that normally have spots when they were transferred from a freezer to formalin.

DARKNESS OF ANAL FIN (Table 5).—The anal fin is most often moderately dark in large-scaled menhadens, whereas that of *smithi* usually has little or no color. The consistent difference between the parental species and the general intermediacy of the hybrid in any particular geographic area indicates that the differences are genetically controlled. Large-scaled menhadens from the peninsular Florida coasts have a darker anal fin than northern samples. In general menhaden from the gulf coast of Florida are darker than the cognate on the Atlantic coast. The darkest anal fins for large-scaled menhadens, *smithi* and hybrids are found in specimens from along northwest peninsular Florida at Horseshoe Beach, Steinhatchee, and Suwannee. Hybrids from Florida Bay also have a dark anal fin. The specimens of *gunteri* had been preserved for many years and because of the possibility of fading they were not compared.

YELLOW ON BODY, ANAL FIN AND OVARIES.—This character was analyzed on fresh specimens from the Indian River, Florida. *B. tyrannus* has a somewhat yellowish body, caudal fin, anal fin, and ovaries. *B. smithi* has a whitish or "milky" colored body, white ovaries, little or no yellow on the anal fin, but has a yellow caudal fin. Hybrids are somewhat yellowish in body color and generally are intermediate in anal fin color; they lack ovaries. The bright yellow caudal fin of *smithi* accounts for the name "yellowfin menhaden". In *tyrannus* the melanin is more conspicuous than xanthin, at least on the caudal fin margins.

Table 5. Darkness of Anal Fin, Expressed in Percentages

Locality	N	A	B	C	D
B. tyrannus					
New Jersey	37		8	89	3
Chesapeake Bay	51		10	82	8
North Carolina	29	3	31	63	3
Fernandina	97	2	19	63	16
Indian River	43			84	16
Jupiter	2			100	
B. smithi × *tyrannus*					
Indian River	23		43	57	
Jupiter	3			100	
B. smithi					
Indian River	28	89	11		
Jupiter	6	83	17		
Florida Bay	23	83	17		
Charlotte	28	100			
Sarasota	21	62	24	14	
Horseshoe	11	27	36	36	
Steinhatchee	29	28	10	62	
Apalachicola	27	56	19	26	
B. smithi × *patronus*					
Florida Bay	16			31	69
Charlotte	3		67	33	
Sarasota	58	16	36	48	
Steinhatchee	27			4	96
Horseshoe	12			33	67
Apalachicola	5			100	
B. patronus					
Sarasota	7		57	29	14
Steinhatchee	29			38	62
Horseshoe	14			50	50
Apalachicola	17		12	76	12
Louisiana	49	47	24	29	
Texas	41	73	24	3	

Key: A, melanin lacking. B, a few scattered melanophores. C, fin dusky. D, fin distinctly blackish on at least anterior half.

MERISTIC CHARACTERS

The most important meristics for separating hybrids are enumerated in Tables 1 and 2. Hybrids were separated from the parental species on the basis of field characteristics, but many meristic characters are useful for separating sympatric forms.

PREDORSAL SCALES (Table 6).—This character is useful for separating *smithi* from *tyrannus* and *smithi* x *tyrannus*. On the gulf coast *smithi* x *patronus* is intermediate and usually can be separated from both parental species by this character.

VERTEBRAE (Table 7).—*B. tyrannus* usually can be separated from the other forms in the Indian River by this character, but all three forms occurring on the gulf coast usually have 44 or 45 vertebrae.

LATERAL SCALE ROWS (Table 8).—Hybrids from the Atlantic and gulf usually can be separated from *smithi* by this character. Indian River hybrids have a significantly higher number of lateral scale rows than *tyrannus*. On the gulf coast the hybrids are similar to *patronus*, except for a significantly higher number in the Steinhatchee sample. Scales may be slightly smaller in the hybrid than in the large-scaled menhadens but no obvious difference exists.

GILL FILAMENTS ON CERATOBRANCHIAL ARCH (Table 9).—This character separates *tyrannus* from all the other Atlantic and gulf forms. It is useful to a lesser degree to separate *patronus* from *smithi* and from *smithi* x *patronus*.

OPERCULAR STRIATIONS (Table 10).—The number of ridges is most useful for separating hybrids from *smithi*. Hybrids usually can be separated from the large-scaled species by the appearance of the opercular ridges; the ridges appear to be wider, straighter, less uniform, and fewer in number in the hybrids.

Table 11 is a meristic comparison of hybrids with parental species. Hybrids are intermediate in predorsal scales, dorsal rays, and opercular striations. For anal rays and pectoral rays, the parental species are not significantly different from each other at most localities but both hybrids have significantly higher numbers than the parental species in most comparisons. Whether or not this is heterosis depends on how the term is defined. A new gene combination in the hybrids is likely to produce a different number of elements, if the parent species are genetically different although morphologically similar. For those characters in which the parental species are very different, the hybrids are intermediate or correspond to one of the parental species.

Table 6. Numbers of Predorsal Scales

Locality	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	N	X	SD
B. tyrannus																																
Massachusetts						1	2	1	3	9	2	5	2	6		4														35	38.5	2.69
New Jersey							1	3	4	5	10	4	7	10	1	1	1	1												48	38.9	2.41
Chesapeake Bay						2		3	1	4	8	5	8	6	6	3	4													50	39.5	2.75
North Carolina								2	2		6	5	7	5	2	1														30	39.2	2.00
Fernandina						1	1	5	5	5	3	10	5	11	2	2	1													51	38.7	2.57
Indian River							1	6	3	3	8	16	9	9	3		2		1											61	39.0	2.38
Jupiter									1				1																	2	38.0	
B. smithi × *tyrannus*																																
Indian River									3	1	3	7	12	8	10	8	7	7	3	2	1	1								73	41.9	2.84
Jupiter												1	1			1														3	40.7	
B. smithi																																
North Carolina																	2	1		1	2	4	1							11	47.5	3.21
Indian River													1			1	2	3	4	6	8	7	3	4	2	3	1		1	46	48.4	3.07
Jupiter																			2	1		1	1		1					6	48.3	
Florida Bay												1	1	4	1			3	2	6	2	2	1		1					24	45.4	3.34
Charlotte												1	1		5	2	4	5	2	4	2	1	1			1	1			30	45.3	3.25
Sarasota										1		2	3	6	8	2	5	10	10	10	6	2	1	1			1			68	44.8	3.15
Steinhatchee													4	2	1	5	7	11	6	8	3	2		1						50	44.9	2.48
Apalachicola											1	2		4	2	2	6	10	5	4	5	6		1						48	45.1	2.97
Alabama															1							1								2	45.5	

B. smithi × *patronus*																												
Florida Bay					1		2	1		3	2	2	4													15	37.3	2.55
Charlotte								1		1	3	3	2	1												11	38.5	1.64
Sarasota						1	1	2	6	7	12	12	8	5	1	4										59	38.6	2.19
Steinhatchee					1	1	1	2	4	10	5	7	10	5		2										48	38.3	2.35
Apalachicola								1	1		1	1	2	1		1										8	39.0	
B. patronus																												
Sarasota				2	1	1	3		2	1																10	33.8	2.11
Steinhatchee		3	3	3	7	9	14	7	1	2		1														50	33.2	2.08
Apalachicola		2	4	3	10	3	10	7	3	2	1															45	33.2	2.18
Louisiana	1	3	3	9	11	8	6	4	2	1																48	32.4	1.97
Texas		3	3	6	6	4	3	1		1																27	31.9	1.91
B. gunteri																												
Louisiana													2		3	4	4	6	2	7	1	1		1		31	44.9	2.50
Texas												1	3	2	2	5	4	3	4	3	4				1	32	44.4	2.97
Campeche															1	1			1			2				5	45.8	

Table 7. Numbers of Vertebrae[1]

Locality	41	42	43	44	45	46	47	48	49	N	X	SD	SE
B. tyrannus													
North Carolina[2]					2	179	1226	230	1	1638	47.03	.506	.012
Indian River				1	4	14	33	7		59	46.70	.837	.108
B. smithi × *tyrannus*													
Indian River				8	20	9				37	45.03	.687	.112
B. smithi													
North Carolina[3]				3	9	1				13	44.85	.557	.155
Indian River				4	18	4				26	45.00	.566	.110
Florida Bay				10	6					16	44.38	.496	.124
Naples			1	15	6					22	44.23	.529	.112
Louisiana[4]			1	15	9					25	44.32	.555	.111
B. smithi × *patronus*													
Florida Bay					10					10	45.00		
Steinhatchee				2	10	3				15	45.07	.598	.154
B. patronus[5]													
Suwannee				5	10					15	44.67	.484	.125
B. gunteri													
Louisiana[4]		14	16							30	42.53	.508	.092
Texas	1	12	9							22	42.36	.580	.123

[1] To be consistent with a recent study (June, 1965) the hypural bones are not counted.
[2] From June (1965).
[3] From Hildebrand (1948).
[4] From Christmas and Gunter (1960).
[5] Hildebrand's (1948) vertebral counts on *patronus* from the Gulf of Mexico are omitted because they appear to include *gunteri* specimens.

Table 8. Numbers of Lateral Scale Rows

Locality	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	N	X	SD
B. tyrannus																																												
Massachusetts				1		2		4	3	1	7	4	2	3	1	1		1	1																							31	50.2	3.37
New Jersey	1			1	3	5	7	13	5	4	3																															42	46.6	1.99
Chesapeake Bay							4	7	11	10	6	4	3			1																										46	48.8	1.88
North Carolina						3	5	4	5	7	3	1																														28	47.8	1.69
Fernandina					2	2	7	15	11	10	3		1	1																												52	47.7	1.71
Indian River			2	7	7	11	10	12	10	2			1																													62	45.8	1.97
Jupiter									1	1																																2	48.5	
B. smithi × *tyrannus*																																												
Indian River			1	1	5	1	2	3	3	6	8	8	4	6	3	4	2	5	2	3	1	2		1																		71	51.7	5.10
Jupiter									2		1																															3	48.7	
B. smithi																																												
North Carolina																								2	2	1		1	3	3												12	66.4	2.43
Indian River																									2	2	1	3	4	5	7	6	4	5	3	2						44	70.1	2.86
Jupiter																											1			1				2					1		1	6	73.2	
Florida Bay																			1	1	1	2		3	4		2	2	2	3	1	2	1									25	65.5	3.94
Charlotte																	1	2	1	9	1	3	5	1		3	1	1			1											29	61.1	3.28
Sarasota																		1	5	4	4	3	4	8	10	2	4	8	2	3	2	1	1	1	1		1					65	64.3	4.23
Steinhatchee																4	2	3	4	6	5	1	6	7	4	2	1	2		1												48	60.8	3.48
Apalachicola															1	2		3	3	6	1	3	5	3	4	4	3	1		1	1	2										43	62.0	4.22
Alabama																				1				1																		2	61.0	
B. smithi × *patronus*																																												
Florida Bay								1	4	1	4	2		2		1																										15	50.1	2.25
Charlotte						1	1	3	4	1	2																															12	47.8	1.48
Sarasota			2	6	13	13	6	8	4	6	1																															59	45.5	2.00
Steinhatchee			1	4	3	6	4	16	4	4	3	1	3																													49	46.9	2.42
Apalachicola				3	1	1	1	2																																		8	44.8	
B. patronus																																												
Sarasota				1	5		3																																			9	44.6	1.12
Steinhatchee			3	5	9	16	9	6	2																																	50	45.0	1.48
Apalachicola			1	9	15	6	11	6																																		48	44.7	1.39
Louisiana			1	3	6	13	9	4	4																																	40	45.4	1.46
Texas				5	6	7	7	1																																		26	44.7	1.18
B. gunteri																																												
Louisiana																								1		2	2	3		6	8	3	1	1	1		1					29	69.2	2.77
Texas																					2	1	1	1	1	1	3	3	2	5	2	2	3		1							28	67.4	3.77
Campeche																										1		1	1	1	1											5	67.8	

Table 9. Numbers of Gill Filaments on the Ceratobranchial Arch

Locality	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	N	X	SD
B. tyrannus																																			
Massachusetts																					1	1	4	2	1	1							10	57.4	1.43
New Jersey																			2	2	5	7	3	11	6	9	1	1		1		1	49	57.9	2.93
Chesapeake Bay																		1	2	7	6	7	6	8	5	4		1	1	1		1	50	57.1	2.88
North Carolina																		1		2	2	3	9	6	1	2	2		1		1		30	57.6	2.65
Fernandina																	1	1	3	6	6	3	5	5	8	3	1	3	1	2			48	57.3	3.21
Indian River																			3	1	6	5	12	4	8	8	7	3	4	3	1		65	58.7	2.95
Jupiter																					1		1										2	56.0	
B. smithi × *tyrannus*																																			
Indian River						2	1	7	14	12	13	6	6	2	5	3	1				1												73	45.0	2.73
Jupiter											2			1																			3	46.0	
B. smithi																																			
North Carolina						1	1			1	3	4	2																				12	44.8	2.21
Indian River					1	1	2	3	6	8	3	6	7		3	4	1	2															47	45.5	3.15
Jupiter								2		1	1	1			1																		6	44.7	
Florida Bay				1	3	4	5	3	3	2	3	1																					25	41.8	2.55
Charlotte	1			2	2	6	3	1	3	5	5		1																				29	41.9	2.79
Sarasota	1		2		4	6	8	7	11	13	5	4	1	1	2	1																	66	42.8	2.83
Steinhatchee			1	1	4	2	9	7	2	6	11	3	1	1																			48	42.8	2.53
Apalachicola		1	1		2	2	1	9	6	5	7	7	4	2		2																	49	43.8	2.97
B. smithi × *patronus*																																			
Florida Bay					1	6	3		5																								15	41.1	1.45
Charlotte				1	1		5		1	3			1																				12	42.0	2.49
Sarasota				2	4	9	8	14	3	8	3	2	2	1																			55	42.1	2.32
Steinhatchee				1	3	3	5	7	7	9	6	4	3	2																			50	43.2	2.43
Apalachicola					1			1	1	2	3																						8	43.4	2.07
B. patronus																																			
Sarasota									1		1		2	1	3			1															9	47.7	2.60
Steinhatchee								1	1	2	1	1	9	4	7	8	5	4	4		3												50	49.2	2.86
Apalachicola									1	3	3	5	8	5	7	6	2	6	1		2												49	48.4	2.74
Louisiana							1	1			3	2	3	7	6	6	3	9			2	2											45	49.3	3.07
Texas									1	3	5	5	3	3	1	4	1																26	46.7	2.24
B. gunteri																																			
Louisiana				1		1		4	3	6	5	5	4			1		1															31	44.6	2.70
Texas					1	5	1	2	7	3	1	3	2	1	2																		28	43.6	2.86

Table 10. Numbers of Opercular Striations[1]

Locality	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	N	$\bar{X}$	SD
B. tyrannus																																					
Massachusetts															2	1		3	5	4	3		1		4	3	2			1					29	20.5	3.95
New Jersey																		5	3	4	9	11	4	4	1	4	1	3							49	21.2	2.73
Chesapeake Bay																	1	4	2		3	2	9	4	8	5	3	3	1	1		2		1	49	23.3	3.76
North Carolina																1	2	1	4	5	3	2	3	3	3		1	2							30	20.7	3.12
Fernandina															1	7	4	0	5	6	5	6	7	3	4	1	1								50	19.7	3.13
Indian River													1		4		4	7	7	10	7	4	7	3	3	1	1	4				1			64	19.9	3.68
Jupiter																					1											1			2	25.5	
B. smithi × *tyrannus*																																					
Indian River											7	7	9	13	6	8	6	6	2	3	2		1	1											71	14.1	3.01
Jupiter												1		1			1																		3	13.1	
B. smithi																																					
North Carolina			1	1	1	2	2	1	1	3																									12	6.1	2.39
Indian River	1			4	5	7	7	10	3	3	4		1																						45	6.3	2.38
Jupiter		1					1	2	2																										6	7.0	
Florida Bay		1						3		8	4	7	1		1																				25	9.5	2.38
Charlotte		2		1	5	3	4	6	3	1	2	1	1																						29	6.3	2.67
Sarasota	1		1	1	4	7	12	9	7	9	6	6	3																						66	7.4	2.55
Steinhatchee	2	1	3	4	6	9	4	10	3	6	2																								50	5.6	2.53
Apalachicola		1	1	5	3	8	9	9	2	7		4		1		1																			51	6.6	2.81
Alabama							2																												2	6.0	
B. smithi × *patronus*																																					
Florida Bay																1	3	2	2	6					1										15	18.1	2.15
Charlotte													5	3	2	2																			12	13.1	1.16
Sarasota										1		2	6	6	7	7	12	7	4	2	1	2	2												59	15.4	2.77
Steinhatchee											4	2	6	6	4	7	5	7	3	2	1		1		1										49	14.9	3.10
Apalachicola												1	1	1		2	1				1	1													8	15.4	3.57
B. patronus																																					
Sarasota														1		1	1	2			1	3	1												10	18.3	3.09
Steinhatchee													2	3	2	3	5	8	3	6	6	3	2	1	2	1	1	1		1					50	18.5	3.82
Apalachicola														2	2		6	8	4	7	4	5	1	2	1	2	2	1	1						48	19.3	3.68
Louisiana															2	1	10	5	5	4	5	2	4	3	1	3	1	2				1			49	19.7	3.85
Texas													1				2	3	4	4	5		3	3	1	1									27	19.5	2.89
B. gunteri																																					
Louisiana					1	1	2	9	4	6	3		1	2	1																				30	8.4	2.33
Texas	1	1	1			4	1	1	4	4	5	3	3	1					1																30	8.5	3.75
Campeche										1	2				1			1																	5	12.0	

[1] Smaller specimens (all of those from Florida Bay and Gulf of Campeche) have a high number because this count is inversely related to length of fish in these forms

Table 11. MEANS OF COUNTS IN *Brevoortia* FROM THE ATLANTIC AND GULF COASTS OF FLORIDA

Character	Indian River			Florida Bay		Charlotte Harbor		Sarasota			Steinhatchee			Apalachicola		
	T	SXT	S	SXP	S	SXP	S	P	SXP	S	P	SXP	S	P	SXP	S
Vertebrae	46.7*	45.0	45.0	45.0	44.4							44.7	45.1			
Predorsal scales	39.0*	41.9*	48.4	37.3*	45.4	38.5*	45.3	33.8*	38.6*	44.8	33.2*	38.3*	44.9	33.2*	39.0*	45.1
Scutes	32.8*	31.8	31.8	31.0	30.8	31.2*	30.9	30.4	30.9	30.9	30.0*	30.7	30.8	30.1	30.6	30.8
Lateral scales	45.8*	51.7*	70.1	50.1*	65.5	47.8*	61.1	44.6	45.5*	64.3	45.0*	46.9*	60.8	44.7	44.8*	62.0
Gill filaments	58.7*	45.0	45.5	41.1	41.8	42.0	41.9	47.7*	42.1	42.8	49.2*	43.2	42.8	48.4*	43.4	43.8
Dorsal rays	16.7*	15.8*	15.1	15.9*	14.8	16.0*	14.8	15.9	15.6*	14.8	16.1*	15.6*	15.0	16.1	16.2*	15.0
Anal rays	19.0*	19.6	19.4	19.6	19.1	19.8	18.9	18.6*	19.6*	18.9	19.0*	19.7*	19.0	19.1*	20.5*	19.1
Pectoral rays	16.6*	15.7	15.4	15.9	15.4	15.8*	15.2	15.1	15.5*	15.0	15.3*	15.8	15.4	15.3*	16.2*	15.1
Opercular striations	19.9*	14.1*	6.3	18.1*	9.5	13.1*	6.3	18.3*	15.4*	7.4	18.5*	14.9*	5.6	19.3	15.4*	6.6

Key: P=*patronus*. S=*smithi*. SXP=Hybrid *smithi* × *patronus*. SXT=Hybrid *smithi* × *tyrannus*. T=*tyrannus*.
*=a significant difference.

Hybrid indices of meristic characters (Table 11) are based on values of zero for *tyrannus* and *patronus* and one hundred for *smithi*. Anal rays and pectoral rays were not utilized because hybrids have extreme values. Vertebral counts were not utilized because of limited data. Hybrid indices are somewhat intermediate: 60 for Indian River (*smithi* x *tyrannus*), 53 for Sarasota Bay, 52 for Steinhatchee, and 42 for Apalachicola (all *smithi* x *patronus*).

Hybrids are compared to parental species for means of proportional characters in Table 12. The similarity of the hybrids to the parental species is evidence of their hybrid status. Of 36 comparisons, hybrids are not significantly different from either parent for 12 comparisons. Hybrids are different from one of the parental species in 18 comparisons. Of 6 comparisons in which hybrids are different from both parent species, the hybrids are intermediate in 4 and extreme in 2.

Comparisons of behavior and ecology

Menhaden forms are compared in regard to extent of migration, schooling behavior, and activity level. Observations by commercial fishermen in Florida were of limited value because they do not recognize an intermediate form of menhaden (a hybrid). They have different common names for two forms along both coasts of Florida.

Both large-scaled species migrate to deeper water in the winter (Hildebrand, 1963; Roithmayr and Waller, 1963). Less offshore migration occurs to the south in *tyrannus*. Large schools of *tyrannus* migrated offshore to the coast of North Carolina to spawn in autumn, and then disappeared (June, 1965). According to Hildebrand (1963), small to medium-sized specimens were present in Chesapeake Bay throughout the year, but their numbers were greatly reduced in the winter. Specimens less than 150 mm were present in Beaufort Harbor, North Carolina all winter (Hildebrand, 1963). In the Indian River on the Atlantic coast of Florida, fishermen caught adult *tyrannus* throughout the winter, as discussed later; these were commonly over 180 mm standard length.

In the Mississippi River Delta region, adult *patronus* start moving offshore in October and occupy deeper waters throughout the winter (Roithmayr and Waller, 1963). Suttkus (1956) indicates that zero class individuals leave Lake Pontchartrain somewhat earlier, in August, September, or October. Adult specimens of *patronus* have been collected near shore on the peninsular gulf coast in the winter,

Table 12. MEANS OF PROPORTIONS IN *Brevoortia* FROM THE ATLANTIC AND GULF COASTS OF FLORIDA EXPRESSED AS PER CENTS OF STANDARD LENGTH

	Indian River			Sarasota			Steinhatchee			Apalachicola		
Character	T	SXT	S	P	SXP	S	P	SXP	S	P	SXP	S
Body depth	34.8*	36.9*	37.8	37.9	36.7*	38.9	39.4*	37.2	37.1	37.2	35.1	37.2
Head depth	27.0	27.3	27.7	28.2*	26.8*	27.6	28.9*	27.0	26.8	28.7	26.7	27.4
Head length	30.8*	29.4	29.5	29.7*	28.7	29.3	30.3*	28.7	28.7	30.9	28.7	29.2
Pect. fin length	19.2	19.1	19.3	19.5	19.2	19.6	19.7	19.6	19.7	19.6	19.1	19.4
Anal fin length	16.6*	18.7	18.8	17.4*	18.4	18.6	17.8*	18.6	18.7	17.5	18.2	19.2
Dorsal fin length	20.2*	19.6*	18.7	20.4*	19.5*	18.7	20.8*	20.0*	19.0	20.4	19.7	19.4
Upper jaw length	14.3*	13.4	13.6	13.9*	13.1	13.3	14.3*	13.4	13.5	14.6	13.1	13.5
Mandible length	16.7*	15.7*	16.4	16.6*	15.5	15.8	16.7*	15.8	15.7	16.9*	15.7	15.9
Caudal ped. depth	9.4	9.6*	10.1	9.0	9.2*	10.2	9.4	9.3*	9.7	9.2	9.0	10.1

Key: P=*patronus*. S=*smithi*. SXP=Hybrid *smithi* × *patronus*. SXT=Hybrid *smithi* × *tyrannus*. T=*tyrannus*. *=a significant difference.

in November (Sarasota Bay, Horseshoe Beach), December (Horseshoe Beach), and February (Tampa Bay).

B. smithi appears to be an inshore or bay form with migrations limited or absent and common near shore along both Florida coasts throughout the year. Adults were collected by fishermen near shore along the gulf coast of Florida in April, May, July, September, October, November, December, and January.

All adult hybrids were collected near shore, always mixed with one or both parental species. Hybrids appear to associate with both parental species near shore, but apparently do not join the large migratory schools of large-scaled menhadens. Hybrids were absent in samples from schools of *patronus* from off Apalachicola and Suwannee and *tyrannus* from off northeastern Florida.

Based on studies in North Carolina, Hildebrand (1963) concluded that *smithi* does not school. This was then the northern edge of the species' range, and it has not been reported there in recent years. *B. smithi* apparently does school where common, as large numbers have been collected in single net hauls around Florida. By the same reasoning, the hybrids probably school.

I noted that juvenile *tyrannus* on the North Carolina coast and juvenile *smithi* (TU 37728) at Naples, Florida, show a similar behavior pattern of swimming in small schools and circling. These schools break up temporarily when the fish are startled. The *tyrannus* schools are more compact and coordinated, but this may be related to the somewhat larger size of the individuals. Compact schools of adult *tyrannus* on the Georgia coast give the appearance of drifting slowly in a uniformly black cloud.

B. smithi and *tyrannus* can be located on a calm day by a characteristic sharp splashing sound produced by flipping the tail at the surface. With fishermen in the Indian River, Florida, I located adult *smithi* in this manner and later caught a sample in a gill net. I recently watched *tyrannus* in small schools on the Georgia coast making a similar noise with their tail, and caught some in a cast net to confirm the identification.

Hildebrand (1963) concludes that *smithi* is a "much more active fish than *tyrannus*" because it makes a vigorous attempt to escape from a seine whereas "*tyrannus* generally strike the net once and then allow themselves to be hauled in without making a further effort to flee." *B. tyrannus* apparently suffocates faster. Fishermen report that when *smithi* escape a gill net they often strike the net again instead of avoiding it. Although *smithi* is more active when caught in a net, *tyrannus* appears to be a more active fish in nature. A higher activity level in *tyrannus* is indicated by its migratory nature, greater lipid reserves (Dahlberg, 1969b), copious mucus, more streamlined or torpedo-shaped body, and apparently faster suffocation when caught in net. *B. tyrannus* has about twice the capacity of *smithi* to store lipids. Hybrid *smithi* x *tyrannus* inherit an intermediate capacity to store lipids (Dahlberg, 1969b). Copious mucus facilitates swimming by reducing friction (van Oosten, 1957) in *tyrannus* and *smithi* x *tyrannus*. Mucus is relatively sparce in *smithi*.

Discussion of Hybridization of Menhadens

Hybridization is rare in marine fishes and in the family Clupeidae. Lagler *et al.* (1962) list only 11 American marine fish hybrids, representing eight families. Feddern (1968) recently described hybrid angelfishes from off southern Florida. Minckley and Krumholz (1960) describe hybrids between two primarily freshwater clupeids of the genus *Dorosoma* (the two forms sometimes considered as separate genera). The hybridization of one form with two others, found in menhadens, is unusual, with hybrids of *smithi* and *tyrannus* on the Atlantic coast of Florida and hybrids of *smithi* and *patronus* on the gulf coast of Florida. Application of the term "hybrid" to these two new forms is equivocal because of their abundance and extensive backcrossing, but their hybrid origin is unequivocal.

Evidence for hybridization and introgression.—Evidence for hybridization is circumstantial. The predominance of males seems to be the best evidence that the new forms are hybrids and not new species. These males do not result from segregation of the sexes in an undescribed species because females did not occur in collections with male specimens that were running milt. The one female hybrid from the Indian River represents less than one per cent of the hybrids for which sex was determined. This observation was verified by Hettler (1968) for the gulf coast hybrid form. Hybrid menhadens are intermediate in hybrid indices of meristic characteristics, general appearance, frontal groove (Table 3, Fig. 4), ventral fin shape, and fat content (Dahlberg, 1969b). Turner (1967) and Hettler (1968) report viable yolk-sac larvae from an artificial *smithi* x *patronus* cross.

Several circumstances suggest that backcrossing and introgression are likely. Both hybrid combinations are abundant (Tables 13 and 14). When the parental species were spawning in the Indian River, hybrids were running milt. The distinctive characters of the Indian River population of *tyrannus* and Sarasota Bay *patronus* appear to

Table 13. RELATIVE ABUNDANCE OF TWO SPECIES AND HYBRIDS OF *Brevoortia* IN GILL NET CATCHES BROUGHT TO DOCK AT SEBASTIAN ON THE INDIAN RIVER, FLORIDA

Date	*B. tyrannus*	hybrid	*B. smithi*
15 May 1965	common	abundant	common
12 Sept. 1965	abundant	abundant	common
18 Oct. 1965	common	abundant	uncommon
22 Nov. 1965	uncommon	common	common
14 Dec. 1965	common	abundant	common
6 Jan. 1966	uncommon	abundant	abundant
12 Feb. 1966	common	abundant	abundant
10 March 1966	common	abundant	uncommon

result partly from introgression as discussed below. Other evidence for introgression is the presence of a few lateral spots on two specimens of otherwise distinct *smithi* from the gulf coast of Florida (Horseshoe Beach and Sarasota Bay). Yolk-sac larvae have been reared from an artificial backcross between *smithi* and hybrid *smithi* × *patronus* (Turner, 1967; Hettler, 1968).

FACTORS INFLUENCING HYBRIDIZATION.—Divergence of the large-scaled menhadens from the small-scaled menhadens resulted either from geographic isolation or different habitat preferences. The small-scaled menhadens are more inshore forms than the migratory large-scaled menhadens. Gosline (1948) hypothesized that the parent species of hybrid *Menidia beryllina* x *M. menidia* from off northeastern Florida diverged as Atlantic and gulf cognates. He thought that the gulf form subsequently dispersed up the Atlantic coast. It is not likely that the large-scaled and small-scaled menhadens diverged as Atlantic and gulf cognates because the differences between the two groups are not characteristic of trans-Florida isolates. Hybridization of menhadens, silversides, and probably angelfishes is related to the complex geological history of the Florida plateau. Convergence of behavior and overlapping of niches on the emergent Florida plateau resulted in hybridization in menhadens.

Whereas adult large-scaled menhadens occur offshore during winter in northern regions, the warm Florida waters allow adult *tyrannus* to occupy the Indian River during its winter and early

Table 14. NUMBERS OF *Brevoortia* IN SAMPLE COLLECTIONS FROM THE FLORIDA GULF COAST.

	B. smithi	Hybrid	*B. patronus*
Florida Bay, Monroe Co.,			
Buttonwood Canal, Juveniles			
30 Oct. 1963	84	15	—
26 June 1964	78	3	—
Naples, Collier Co.,			
Juveniles 16 May 1965	120	—	—
Charlotte Harbor, Charlotte Co.,			
Adults 15 Nov. 1965	260	3	—
Juveniles 21 May 1964	17	18	—
Adults March 1966	389	48	—
Sarasota Bay, Manatee Co.,			
Alults 9 Nov. 1965	479	58	8
Tampa Bay, Pinellas Co.,			
Adults, several small collections	73	6	2
Suwannee River mouth, Levy-Dixie Co.,			
Adults 1 Sept. 1965	1	—	school
Horseshoe Beach, Dixie Co.,			
Adults 14 Nov. 1965	8	8	3
Adults 12 Dec. 1965	390	7	15
Steinhatchee River, Dixie-Taylor Co.,			
Adults 14 Nov. 1965	153	47	—
5 April 1965	6	1	—
Carrabelle, Franklin Co.,			
Adults 15 May 1965	25	2	common
Port St. Joe, Gulf Co.,			
Adults 9-14 July 1965	53	6	common

spring spawning season. This allows spawning with *smithi* in the Indian River.

B. tyrannus generally spawns in colder water than *smithi*. Table 15 shows the approximate times and mean monthly water temperatures when *tyrannus* and *smithi* spawn along the Atlantic coast. In the northern sector spawning involves two major populations, spring spawners (April and May) in Cape Cod and Long Island waters,

Table 15. Average Monthly Water Temperatures[1] and Estimated Spawning Periods for *Brevoortia* in the North Atlantic

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Spawning range
North Atlantic 1944-1958 Woods Hole, Mass.[2]	35.3	33.8	36.9	*44.7*	*53.5*	*62.7*	*70.2*	*71.2*	*67.8*	*59.9*	51.3	41.2	44.7-71.2
Middle Atlantic 1912-1958 Atlantic City, N. J.[2]	37.3	36.2	*40.0*	*47.3*	*55.9*	64.6	69.3	71.7	*69.7*	*61.3*	51.5	41.6	40.0-69.7
North Carolina 1923-1928 Diamond Shoal Lightship[2]	*61.8*	*60.0*	*58.6*	62.1	70.0	76.0	79.1	80.4	78.3	73.7	*66.8*	*64.4*	58.6-73.7
Florida 1944-1958 Fernandina Beach[3]	*57.6*	*58.8*	*63.4*	69.5	76.5	81.6	83.4	83.6	81.6	74.0	*66.2*	*58.4*	57.6-69.5
Florida 1946-1948 Daytona Beach (ocean)[3]	*61.8*	*62.0*	*64.5*	70.4	75.8	78.9	78.7	78.4	81.5	76.4	71.1	*65.0*	61.8-65.0
Florida 1946-1958 Canova Beach[4]	*65.7*	*65.7*	*68.5*	67.4	76.5	79.3	78.3	79.9	82.4	78.0	73.1	*67.9*	65.7-68.5
Florida 1940-1958 Miami Beach	70.6	71.3	73.7	76.8	80.3	84.1	85.6	86.2	84.1	79.9	75.9	72.9	

[1]From U. S. Coast and Geodetic Survey (1960).
[2]Figures in italics show spawning months of *tyrannus* reported by Higham and Nicholson (1964) and June (1965).
[3]Figures in italics show spawning months of *tyrannus* estimated by author as expected from water temperatures.
[4]Figures in italics show spawning months of *tyrannus* in the Indian River, estimated by author from examination of gonads. Those underlined show spawning time of *smithi* in the Indian River as observed by author.

and autumn spawners (October and November) from Long Island to North Carolina, with little spawning from June through August (June, 1965). Indian River *smithi* spawned primarily in February in 1959 (Reintjes, 1962). In late February and March of 1966, all three forms that occur in the Indian River were running milt, and some *tyrannus* and *smithi* released eggs when pressed. A few specimens of *tyrannus* had enlarged gonads (occupying about two-thirds of the coelom) in December, while *smithi* did not mature to this degree until February. *B. tyrannus* probably spawned from December to March, and *smithi* spawned in February and March. Spawning by the southern fringe *tyrannus* population in the Indian River is limited to the higher levels of its spawning temperature range, during a cold water temperature regime in the winter, which results in an overlap with that of *smithi*.

Length frequencies of juvenile menhaden from the Tampa Bay area were extrapolated to estimate spawning time of the gulf coast menhadens. Data were taken from BCFSP specimens and from Springer and Woodburn (1960). Seven series of *smithi* were spawned in February and March and six series containing both *patronus* and hybrids were spawned in January and February.

Evidence of spawning time was also obtained from the degree of gonad maturity of specimens collected as follows: November 1965 at Charlotte, Steinhatchee, Sarasota, and Carrabelle; December 1965 at Horseshoe Beach; January 1966 at Horseshoe Beach; February 1964 at Tampa Bay; April 1962 at Tampa Bay. Arbitrary stages of maturity based primarily on gonad size are modified from Higham and Nicholson (1964): I—gonads not developing; II—gonads occupying about one-third to one-half of coelom; III—gonads occupying about two-thirds of coelom; IV—gonads occupying about three-fourths of coelom, ready to spawn; V—spawning, or recently spawned and with small gonads.

B. smithi specimens were not ready to spawn (stages II and III) in November, December, and January. Some from Tampa Bay probably spawned (stage IV) in February. Tampa Bay specimens had small gonads in April after the spawning season had ended. *B. patronus* apparently matured and commenced spawning earlier; some reached stages III and IV in November, others were not ready to spawn (stages II and III) in December. Some *patronus* specimens collected in February were mature enough to spawn. Gonad maturity indicates that both parental species and the male hybrids were spawning in the Tampa Bay area in February. Maturation time of hybrids corresponds to that of *smithi* rather than *patronus*, because hybrids had not reached spawning maturity in November or December. A sample of mixed *smithi* (TU 40959) and hybrid *smithi* x *patronus* (TU 40958) caught in Charlotte Harbor and frozen by a fish dealer, were most likely taken in March 1966, but possibly in February or April; both forms were in spawning condition. Analyses of length frequencies and gonadal maturity indicate that spawning by all three forms overlaps in February and March. *B. patronus* may commence spawning in November or December. Frequency of menhaden eggs collected in 1965-66 indicated a spawning peak in February off southwest Florida when water temperatures were 63° to 70°F. (Turner, 1967). Most eggs were probably *smithi*. All three forms were ripe in March in two collections when water temperatures were 68° and 73°F. (Hettler, 1968). Nothing suggests that gulf and Atlantic menhaden cognates spawn at different times or water temperatures when they occur at the same latitude.

Hubbs and Kuronuma (1942) cite an abundance of both parental species and generalized spawning habits as probable factors in hybridization of marine flounders. In the Indian River *smithi* was consistently common and *tyrannus* was sporadically abundant during the spawning season. I saw large gill net catches of both species and the hybrids from the Indian River, consisting predominantly of ripe fish. The generalized habit of spawning in schools, which occurs in *tyrannus* (Hildebrand, 1963) and probably in *smithi*, favors hybridization.

GEOGRAPHIC VARIATION IN RELATIVE ABUNDANCE OF FLORIDA MENHADEN POPULATIONS.—Available specimens indicate geographic variation in relative numbers of the parental species and hybrids. Both parental species and hybrid *smithi* x *tyrannus* were noted on all monthly trips to a fish dealer on the Indian River from May 1965 to March 1966. The terms "abundant", "common" and "uncommon" in Table 13 refer to the relative numbers of the three forms caught at night in gill nets and brought in the following morning. Most catches included several 130-pound boxes or more of menhaden. Reintjes (1960) indicated that *tyrannus* frequently appeared in catches from Indian River in fall and winter. Although sporadically abundant, *tyrannus* appears to be the least plentiful of the three forms in the commercial catch. *B. tyrannus* may be more plentiful than collections indicate because they appear to average smaller in size than *smithi*, and would thus be less vulnerable to the gill net fishery. The menhaden bait fishery of the Indian River relies primarily on *smithi* and the hybrid. The hybrid was found common or abundant in all catches examined. *B. tyrannus* is abundant on the Georgia coast where *smithi* and the hybrid are uncommon.

Table 14 shows the relative numbers of *patronus, smithi,* and their hybrids obtained from the gulf coast of Florida. Off the Florida panhandle the hybrids are the least plentiful of the three forms. Fishermen state that *patronus* is seasonal in occurrence. Adult *smithi* were obtained from the Florida panhandle to the mouth of the Suwannee River in all four seasons.

Southward along the Florida gulf coast *patronus* tends to be replaced by *smithi* and hybrid *smith* x *patronus*. Schools of *patronus* have occurred seasonally south to Cedar Keys and sporadically south to Tampa Bay (Reintjes, 1964a). Records of adult *patronus* from near Naples and juveniles from Cape Sable (Reintjes, 1964a) may be based on hybrids. Hettler (1968) reported *patronus* south to Naples. Tabb and Manning (1962) recorded no *patronus* from Florida Bay. The scarcity of *patronus* in the collections of juvenile *smithi* and hybrids from Charlotte Harbor and Tampa Bay indicates they are rare in this region or sporadic in occurrence. Of 1,753 menhadens collected off southwest Florida in 1966 (Turner, 1967) 56% were *smithi,* 7% were *patronus* and 37% were "menhaden with many characteristics intermediate." Composition of two collections from off Naples and Sanibel Island (Hettler, 1968) were respectively 74% hybrids, 17% *patronus*, and 9% *smithi*; and 41% hybrids, 5% *patronus*, and 54% *smithi.* Identification of 8 specimens (1.5%) from Sarasota Bay as "good" *patronus* apparently was correct, even though they were collected with 479 *smithi* (88%) and 58 hybrids (10%), and gonads of all three forms were well developed. Their characters were those of *patronus* and they included both sexes (6 females and 2 males). All the hybrids were males and the *smithi* sample included both sexes. These findings confirm Reintjes' (1964a) conclusion that the menhaden fishery off southwest Florida is supported principally by *smithi.* Hybrids are more plentiful than *patronus* between Tampa Bay and Florida Bay.

Complete fusion of the interbreeding species is prevented by the decreased reproductive potential of the hybrids resulting from the absence of females. Off southwest Florida the hybrids would eventually be eliminated by the abundant *smithi* unless *patronus* genes were regularly incorporated, or unless *smithi* and hybrids represent a somewhat stable sexually dimorphic population. Although the latter is common in fishes, the males do not normally originate from hybridization.

Somewhat complementary sex ratios may have resulted from extensive backcrossing with *smithi*. In a mixed sample of 389 *smithi* and 48 hybrid *smithi* × *patronus* from Charlotte Harbor, all hybrids were males and the sample of *smithi* was predominantly (85%) females. A second possible explanation for the unequal sex ratio in *smithi* is that fishing gear, either gill nets or seines in this case, is selective for females, which may average larger than males, as in some other clupeid fishes.

Geographic Variation and its Relationship to Water Temperature

Data from samples are arranged to show geographic variation of proportions in Tables 16 and 17, and of counts in Tables 6-10, 18-21. For statistical analyses of larger samples see Tables 22, 23, and 24.

Variation within and between fish populations can often be attributed to the effect of environmental factors on the developing embryo (Hubbs, 1926; Gabriel, 1944; Lindsey, 1954; Barlow, 1961; and references therein). The relationship to water temperature is usually direct for body proportions and inverse for meristic characters. Opposite effects and V-shaped curve effects also occur. Some biological characters vary with water temperature. The hypothesis that geographic differences between closely related menhaden populations result primarily from differences in temperature during embryonic development is reasonable because 1) at any given time other environmental factors are either relatively uniform over the range of different populations or highly variable within a population, as opposed to the relatively clinal variation of water temperature; 2) modification of characteristics by temperature has been demonstrated; 3) the expected patterns are predominant in menhadens; 4) other marine fishes show similar variation.

The effect of water temperature on characters is demonstrated by geographic variation in *tyrannus* and by comparisons of *tyrannus* and *patronus*, Atlantic and gulf populations of *smithi*, and *smithi* and *gunteri* (Tables 22, 23). Furthermore the greater divergence of the large-scaled cognates compared to the small-scaled cognates can be attributed to the greater latitudinal difference in the centers of abundance of large-scaled than small-scaled menhadens, and the corresponding difference in average water temperature during development.

Table 16. *Brevoortia* BODY AND HEAD PROPORTIONS[1]

Locality	N	C.P.D.	B.D.	H.D.	H.L.	U.J.L.	M.L.
B. tyrannus							
Massachusetts	11-12	8.85	33.4 (2.37)	26.8 (.876)	32.2 (.665)	15.2 (.436)	17.9
New Jersey	47-50	9.10 (.325)	33.8 (1.12)	26.8 (.380)	31.7 (.720)	14.7 (.518)	17.2 (.453)
Chesapeake Bay	43-45	8.99 (.359)	32.6 (1.43)	27.4 (.736)	32.4 (.845)	15.0 (.491)	17.4 (.674)
Indian River	63-65	9.41 (.410)	34.8 (1.61)	27.0 (.913)	30.8 (1.056)	14.3 (.621)	16.7 (.765)
Jupiter	1-2	9.70	35.8	26.2	29.9	13.5	16.6
B. smithi × *tyrannus*							
Indian River	65-70	9.57 (.441)	36.9 (1.17)	27.3 (.911)	29.4 (.776)	13.4 (.485)	15.7 (.475)
Jupiter	3	8.97	35.1	26.3	28.7	13.3	15.7
B. smithi							
North Carolina	12	10.23 (.474)	38.4 (1.62)	28.0 (.735)	29.8 (.642)	13.9 (.429)	16.8 (.495)
Indian River	43-47	10.14 (.318)	37.8 (1.25)	27.7 (.624)	29.5 (.830)	13.6 (.446)	16.4 (.518)
Jupiter	6	10.23	37.2	27.2	28.7	13.1	15.7
Sarasota	41-52	10.17 (.369)	38.9 (1.22)	27.6 (.641)	29.3 (.707)	13.3 (.530)	15.8 (.562)
Steinhatchee	49-50	9.73 (.383)	37.1 (1.50)	26.8 (.768)	28.7 (.592)	13.5 (.474)	15.7 (.409)
Apalachicola	50-51	10.10 (.410)	37.2 (1.38)	27.4 (.632)	29.2 (.731)	13.5 (.588)	15.9 (.544)
Alabama	2	10.30	37.2	27.8	29.6	13.9	15.9
B. smithi × *patronus*							
Sarasota	57-60	9.21 (.308)	36.7 (1.52)	26.8 (.755)	28.7 (.788)	13.1 (.513)	15.5 (.562)
Steinhatchee	48-50	9.28 (.369)	37.2 (1.41)	27.0 (.889)	28.7 (.618)	13.4 (.421)	15.8 (.534)
Apalachicola	7-8	8.99	35.1	26.7	28.7	13.1 (.963)	15.7
B. patronus							
Sarasota	10	8.99 (.900)	37.9 (1.36)	28.2 (.735)	29.7 (.831)	13.9 (.428)	16.1 (.554)
Steinhatchee	47-50	9.38 (.295)	39.4 (1.09)	28.9 (.600)	30.3 (.750)	14.3 (.443)	16.7 (.495)
Apalachicola	48-49	9.16 (.340)	37.2 (1.49)	28.7 (.700)	30.9 (8.20)	14.6 (.662)	16.9 (.602)
B. gunteri							
Louisiana	29-31	10.12 (.341)	39.2 (1.54)	29.5 (.856)	31.4 (.667)	15.5 (.517)	18.7 (.642)
Texas	30	10.45 (.521)	38.9 (1.28)	30.5 (.909)	32.2 (.680)	16.0 (.453)	18.9 (.617)

Key: B.D.=Body depth, C.P.D.=Caudal peduncle depth, H.D.=Head depth, H.L.=Head Length, M.L.=Mandible length, N=Number of specimens, U.J.L.=Upper jaw length.

[1]Expressed as mean per cents of standard length with standard deviations.

Table 17. *Brevoortia* FIN LENGTHS[1]

Locality	N	P.F.L.	A.F.L.	D.F.L.
B. tyrannus				
Massachusetts	7-11	17.9 (.458)	15.2 (.806)	19.4 (.660)
New Jersey	39-49	18.3 (.561)	16.6 (.883)	19.5 (.980)
Chesapeake Bay	42-51	18.4 (.634)	16.5 (.705)	19.3 (.857)
Indian River	48-65	19.2 (.810)	16.6 (.843)	20.2 (.835)
Jupiter	2	18.6	16.8	19.8
B. smithi × *tyrannus*				
Indian River	30-71	19.1 (.608)	18.7 (.813)	19.6 (.937)
Jupiter	2-3	19.7	18.2	19.8
B. smithi				
North Carolina	9-12	19.6 (.755)	18.8 (.883)	19.5 (.569)
Indian River	23-46	19.3 (.768)	18.8 (.933)	18.7 (.788)
Jupiter	6	18.9	20.5	19.5
Sarasota	38-46	19.6 (.860)	18.6 (1.338)	18.7 (.690)
Steinhatchee	36-50	19.7 (.806)	18.7 (.732)	19.0 (.872)
Apalachicola	30-51	19.4 (.973)	19.2 (.925)	19.4 (1.068)
Alabama	2	19.5	18.3	18.5
B. smithi × *patronus*				
Sarasota	26-54	19.2 (.819)	18.4 (.898)	19.5 (.809)
Steinhatchee	30-50	19.6 (.825)	18.6 (1.107)	20.0 (.948)
Apalachicola	8	19.1	18.2	19.7 (.572)
B. patronus				
Sarasota	7-10	19.5 (.755)	17.4 (.577)	20.4 (.801)
Steinhatchee	36-50	19.7 (.648)	17.8 (.979)	20.8 (1.008)
Apalachicola	44-49	19.6 (.686)	17.5 (.938)	20.4 (.829)
B. gunteri				
Louisiana	27-31	20.6 (1.086)	20.5 (.806)	19.4 (1.085)
Texas	28	20.5 (.714)	20.8 (1.106)	19.0 (.940)

Key: A.F.L.=Anal fin base length, D.F.L=Dorsal fin base length, N=Number of individuals, P.F.L. = Pectoral fin length.

[1]Expressed as mean per cents of standard length with standard deviations.

MERISTIC CHARACTERS.—Meristic characters are usually inversely related to water temperature in marine fishes. A comparison of menhaden samples (Table 22) shows that 15 significant meristic differences, including all 7 that are highly divergent (78% or more), conform to the inverse relationship, and 8 do not. The direct relationship of four comparisons involving the northern race of *tyrannus* was thought by June (1958) and Sutherland (1963) to be related to

Table 18. NUMBERS OF VENTRAL SCUTES IN *Brevoortia*

Locality	27	28	29	30	31	32	33	34	N	X	SD	SE
B. tyrannus												
Massachusetts			1	3	5	22	7	2	40	31.9	1.019	.161
New Jersey					6	16	19	6	47	32.5	.884	.129
Chesapeake Bay					4	16	22	7	49	32.7	.831	.119
North Carolina					2	15	10	3	30	32.5	.768	.140
Fernandina					9	16	18	4	47	32.4	.894	.130
Indian River					2	19	29	10	60	32.8	.758	.098
Jupiter						1		1	2	33.0		
B. smithi × *tyrannus*												
Indian River			1	6	22	26	9	6	70	31.8	1.095	.131
Jupiter				1		1			2	31.0		
B. smithi												
North Carolina				1	6	5			12	31.3	.674	.195
Indian River				1	17	19	3	3	43	31.8	.810	.123
Jupiter				1	3	1			5	31.0		
Florida Bay				7	14	3			24	30.8	.634	.129
Charlotte				7	17	3			27	30.9	.587	.113
Sarasota			2	18	31	9	2		62	30.9	.828	.105
Steinhatchee			1	15	23	9			48	30.8	.758	.109
Apalachicola			2	10	29	4			45	30.8	.674	.100
Alabama					2				2	31		
B. smithi × *patronus*												
Florida Bay				3	9	3			15	31.0	.648	.167
Charlotte					10	2			12	31.2		
Sarasota			3	7	38	10			58	30.9	.781	.102
Steinhatchee			4	13	26	5			48	30.7	.785	.113
Apalachicola				3	5				8	30.6		
B. patronus												
Sarasota			1	5	3	1			10	30.4	.819	.259
Steinhatchee		1	10	25	12				48	30.0	.742	.107
Apalachicola			6	31	10	1			48	30.1	.636	.092
Louisiana		3	5	28	11	1			48	30.0	.825	.119
Texas			2	15	10				27	30.3	.616	.118
B. gunteri												
Louisiana	1	5	19	4					29	28.9	.681	.126
Texas	1	4	12	7	4				28	29.3	1.023	.193
Campeche		1	2	2					5	29.2		

water temperature, apparently an opposite effect. *B. tyrannus* from north of Long Island, N. Y., spawn primarily in April and May (June, 1965) at lower temperatures than to the south (Table 15).

Table 19. Numbers of Left Pectoral Rays in *Brevoortia*

Locality	14	15	16	17	18	N	X	SD	SE
B. tyrannus									
Massachusetts	1	8	20	12	1	42	16.1	.820	.127
New Jersey		3	15	23	7	48	16.7	.798	.115
Chesapeake Bay		3	21	19	6	49	16.6	.790	.112
North Carolina			9	15	4	28	16.8	.679	.128
Fernandina		2	15	16	5	38	16.6	.785	.127
Indian River		3	22	24	5	54	16.6	.742	.100
Jupiter			2			2	16.0		
B. smithi × *tyrannus*									
Indian River	1	16	33	2		52	15.7	.578	.080
Jupiter		2	1			3	15.3		
B. smithi									
North Carolina		7	5			12	15.4	.513	.148
Indian River	2	26	17	1		46	15.4	.609	.090
Jupiter		3	3			6	15.5		
Florida Bay	1	12	11			24	15.4	.582	.118
Charlotte	3	18	9			30	15.2	.610	.111
Sarasota	13	58	12			83	15.0	.551	.060
Steinhatchee	4	22	23	1		50	15.4	.717	.101
Apalachicola	7	28	13			48	15.1	.639	.092
B. smithi × *patronus*									
Florida Bay		4	9	2		15	15.9	.637	.164
Charlotte		3	8	1		12	15.8	.579	.167
Sarasota	3	24	25	4		56	15.5	.712	.095
Steinhatchee	2	13	28	6	1	50	15.8	.775	.109
Apalachicola		1	2	2		5	16.2		
B. partonus									
Sarasota	1	7	2			10	15.1	.567	.179
Steinhatchee	4	29	13	3		49	15.3	.712	.101
Apalachicola	5	29	15	2		51	15.3	.697	.098
Louisiana	4	21	24	2		51	15.5	.704	.099
Texas	1	17	7			25	15.2	.525	.105
B. gunteri									
Louisiana	3	13	11	2		29	15.4	.780	.144
Texas	4	17	8			29	15.1	.637	.118
Campeche		3	2			5	15.4		

The inverse relationship of six meristic differences between the Atlantic and gulf populations of *smithi* may be related to water temperature because the Atlantic population ranges farther north, to North Carolina, and the gulf population ranges farther south, to

Table 20. NUMBERS OF BRANCHED DORSAL RAYS IN *Brevoortia*

Locality	13	14	15	16	17	18	N	X̄	SD	SE
B. tyrannus										
Massachusetts			2	19	12	2	35	16.40	.694	.117
New Jersey			5	19	19	4	47	16.47	.803	.117
Chesapeake Bay			1	9	32	7	49	16.92	.640	.091
North Carolina			2	15	12	1	30	16.40	.674	.122
Fernandina				14	23	2	39	16.69	.596	.095
Indian River				16	35	2	59	16.66	.540	.070
Jupiter					2		2	17		
B. smithi × *tyrannus*										
Indian River			14	30	3		47	15.77	.580	.084
Jupiter			1	2			3	15.66		
B. smithi										
North Carolina		1	10	1			12	15.00	.425	.122
Indian River		5	31	7			43	15.05	.532	.081
Jupiter			2	4			6	15.67		
Florida Bay		8	14	2			24	14.75	.608	.124
Charlotte		8	20	2			30	14.80	.551	.100
Sarasota		28	44	7	1		80	14.76	.659	.073
Steinhatchee		8	34	7			49	14.98	.551	.078
Apalachicola	1	5	26	7			39	15.00	.649	.104
Alabama			2				2	15		
B. smithi × *patronus*										
Florida Bay			4	7	2		13	15.85	.689	.190
Charlotte			1	10	1		12	16.00	.425	.122
Sarasota		1	22	30	2		55	15.60	.596	.080
Steinhatchee		1	20	27	2		50	15.60	.606	.085
Apalachicola				4	1		5	16.20		
B. patronus										
Sarasota			4	3	3		10	15.90	.874	.276
Steinhatchee		1	6	26	13		46	16.11	.707	.104
Apalachicola			10	26	14		50	16.08	.695	.098
Louisiana			9	26	9		44	16.00	.647	.097
Texas			5	17	3		25	15.92	.570	.114
B. gunteri										
Louisiana		10	16	3			29	14.76	.635	.117
Texas	2	6	18	3			29	14.76	.738	.136
Campeche	1	1	3				5	14.40		

Florida Bay. *B. gunteri* is considered a more southern form than *smithi* because it ranges to the Gulf of Campeche, and may occupy the Caribbean Sea (Reintjes, 1960). Proportions support this latter hypothesis better than meristic characters do.

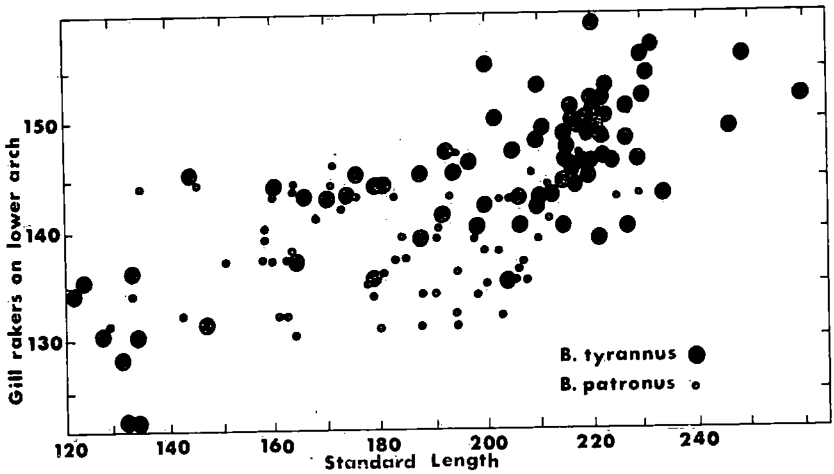


FIGURE 7. Relationship of gill raker numbers to standard length in *Brevoortia tyrannus* and *patronus*.

Numbers of meristic characters are strongly influenced by other factors, as well as water temperature. The number of gill rakers is directly proportional to head size in Pacific herrings (McHugh, 1954), in the genus *Opisthonema* (Berry and Barrett, 1963), and in menhadens. *B. patronus* has a shorter but deeper head than *tyrannus* when expressed as per cent of standard length, and their gill raker counts correspond (Fig. 7), but their gill filament counts are 95% divergent (Table 9). The expected relationship with water temperature occurs with gill rakers and filaments between Atlantic and gulf populations of *smithi*. In a comparison of the gulf population of *smithi* and the large-headed *gunteri*, gill rakers correlate with head size rather than with water temperature, but the number of gill filaments is identical.

Meristic differences between *tyrannus* and *patronus*, which are related to water temperature, have become genetically based. The evidence for this is that the southern fringe of each population, *tyrannus* in the Indian River and *patronus* in Tampa Bay, spawn at similar times and temperatures. The fact that their meristic characters do not converge constitutes evidence that the differences are genetic, and they are maintained by gene flow from northern populations. The consistency of the means of the meristic characters within each species is further evidence for genetic control of the differences.

Induced differences often appear to become genetically based.

Table 21. NUMBERS OF BRANCHED ANAL RAYS IN *Brevoortia*

Locality	16	17	18	19	20	21	22	N	X	SD	SE
B. tyrannus											
Massachusetts			7	13	3			23	18.8	.648	.135
New Jersey			16	15	12	1		44	19.0	.863	.130
Chesapeake Bay			9	19	14	3		45	19.2	.858	.127
North Carolina		5	9	10	3	1		28	18.5	1.026	.194
Fernandia		2	13	26	8			49	18.8	.763	.109
Indian River	1	1	12	24	14	2		54	19.0	.940	.127
Jupiter			1	1				2	18.5		
B. smithi × *tyrannus*											
Indian River		1	9	16	17	12	2	57	19.6	1.136	.150
Jupiter		1			2			3	19.0		
B. smithi											
North Carolina			2	4	5	1		12	19.4	.905	.261
Indian River			3	12	7	3		25	19.4	.866	.173
Jupiter				4	2			6	19.3		
Florida Bay		1	4	7	4	2		18	19.1	1.077	.254
Charlotte		1	7	16	6			30	18.9	.758	.138
Sarasota	2	5	14	28	13	3	2	67	18.9	1.196	.146
Steinhatchee		3	12	19	13	3		50	19.0	.997	.141
Apalachicola		2	11	17	20	1		51	19.1	.917	.128
Alabama			1	1				2	18.5		
B. smithi × *patronus*											
Florida Bay			1	3	6	1		11	19.6	.806	.242
Charlotte		1		2	4	1	1	9	19.8	1.401	.467
Sarasota		2	5	16	29	6	1	59	19.6	.967	.125
Steinhatchee		1	3	15	12	14	3	48	19.9	1.137	.164
Apalachicola				1	2	5		8	20.5		
B. patronus											
Sarasota			6	1	2			9	18.6	.872	.290
Steinhatchee			15	23	9	3		50	19.0	.857	.121
Apalachicola		3	12	17	9	6		47	19.1	1.104	.161
Louisiana		4	19	17	7	3		50	18.7	1.096	.155
Texas		2	11	13	1			27	18.5	.699	.134
B. gunteri											
Louisiana			1	7	8	10	4	30	20.3	1.085	.198
Texas			2	11	9	6	2	30	19.8	1.047	.171
Campeche				1	4			5	19.8		

According to the Baldwin Effect the phenotypic response serves as a "reprieve" until corresponding gene combinations become established by natural selection (Mayr, 1963). He thought this is actually

Table 22. Analysis of Significance of Meristic Differences in *Brevoortia* from North to South

Character	*B. tyrannus*						*B. patronus*		*B. smithi*	*B. gunteri*
	MS — NJ	NJ — CB	CB — NC	NC — FB	FB — IR	IR — WF	WF — LA	LA — TX	AT — GF	GF — GF
Vertebrae	*	0	0	0	†	†92	0	0	†	†99
Predorsal scales	0	0	0	0	0	†90	0	0	†	0
Ventral scutes	*	0	0	0	0	†93	0	0	†	†85
Lateral scales	0	0	0	0	0	0	0	0	†	*
Gill filaments	0	0	0	0	0	†95	0	0	†	0
Dorsal rays	*	0	0	0	0	†	0	0	0	0
Pectoral rays	*	0	0	0	0	†78	0	0	0	0
Anal rays	0	0	0	0	0	0	0	0	0	*
Opercular striations	0	0	0	0	0	0	0	0	0	*
Gill rakers[1]						0			†	*

Key: MS=North of Long Island, N. Y. NJ=New Jersey. CB=Chesapeake Bay. NC=North Carolina. FB=Fernandina Beach. IR=Indian River. WF=Florida west coast . LA=Louisiana. TX=Texas. GF=Gulf of Mexico. *=significant increase to the right (south). O=no significant difference. †=significant decrease to the right (south). Figures show average divergence between two populations.

[1]Gill rakers were not compared statistically but obvious contrasts are presented.

Table 23. Analysis of Differences in Proportions in *Brevoortia*

Characters	Large-scaled species					Small-scaled species					
	B. tyrannus			*B. patronus*		*B. smithi*				*B. gunteri*	
	N.J.	C.B.	I.R.	Su.	Ap.	I.R.	S.B.	St.	Ap.	La.	Tex.
Mean length	222.5	208.0	209.3	198.7	195.0	208.1	197.5	236.9	221.1	230.1	183.6
Body depth	33.8	32.6	34.8†	39.4	37.2	37.8	38.9	37.1	37.2	39.2	38.9
Head depth	26.8*	27.4	27.0†	28.9	28.7	27.7	27.6	26.8	27.4‡	29.5§	30.5
Head length	31.7*	32.4*	30.8	30.3*	30.9	29.5	29.3§	28.7§	29.2‡	31.4§	32.2
Pectoral fin length	18.3	18.4*	19.2*	19.7	19.6	19.3	19.6	19.7	19.4*	20.6	20.5
Anal fin length	16.6	16.5	16.6*	17.8	17.5	18.8	18.6	18.7	19.2*	20.5	20.8
Dorsal fin length	19.5	19.3*	20.2*	20.8	20.4	18.7	18.7	19.0	19.4	19.4	19.0
Upper jaw length	14.7	15.0*	14.3	14.3	14.6	13.6	13.3	13.5	13.5‡	15.5	16.0
Mandible length	17.2	17.4*	16.7	16.7	16.9	16.4*	15.8	15.7	15.9‡	18.7	18.9
Caudal peduncle depth	9.1	9.0*	9.4	9.4	9.2	10.1	10.2§	9.7§	10.1	10.1	10.5

Key: N.J.=New Jersey, C.B.=Chesapeake Bay, I.R.=Indian River, Su.=Suwannee River, Ap.=Apalachicola, S.B.=Sarasota Bay, St.=Steinhatchee, Fla., La.=Louisiana, Tex.=Texas. *=significant difference, †=75-85% divergence, ‡=divergence over 90%, §=difference results from allometric growth.

Table 24. ANALYSIS OF DIFFERENCES IN PROPORTIONS OF SHORTER ADULT *B. tyrannus* FROM CHESAPEAKE BAY TO INDIAN RIVER

Characters	CB	NC	FB	IR
Mean length	180.4	175.5	175.7	180.9
Body depth	33.0	33.8	34.3*	35.6
Head depth	27.6	28.0	28.2*	27.4
Head length	32.7	32.6	32.4*	30.4
Pectoral fin length	18.2*	19.6	19.6*	19.0
Anal fin length	16.7*	16.0	16.4*	17.3
Dorsal fin length	19.0	19.0	19.4	20.0
Upper jaw length	14.9	15.3	15.1*	13.9
Mandible length	17.3	17.7	17.4*	16.3
Caudal peduncle depth	9.1*	9.5	9.5	9.6

Key: CB=Chesapeake Bay. NC=North Carolina. FB=Fernandina Beach. IR=Indian River. *=significant difference.

"the normal process of selection of a polygenic character". Acquired characters could become genetically based in a natural population by "genetic assimilation" (Waddington, 1953) only if they were of adaptive value. Differences between menhaden populations cannot be attributed to natural selection of induced differences because most or all differences related to water temperature would be of doubtful adaptive value. Also, natural selection and water temperature may have opposite effects on characteristics.

PROPORTIONS.—In marine fish proportions are often directly related to water temperature. In an analysis of geographic variation within *tyrannus* and comparisons of *tyrannus* from Indian River with *patronus* from Suwannee, of *smithi* from Indian River with those from Sarasota Bay, and of *smithi* from the Apalachicola area with *gunteri* from Louisiana, 24 significant differences occur (Tables 23 and 24). In 17 (71%) of these comparisons the proportion is greater in the more southern population. Of the 7 comparisons that are inversely related to water temperature, 5 occur between samples of *tyrannus* from northeastern Florida and Indian River, Fla. Distinctive characters of the Indian River population are in part the result of introgressive hybridization with *smithi*. Also the short head, maxillary, and mandible of the Indian River population correspond to those of *patronus*, which suggests an opposite water temperature effect. These shorter proportions may be correlated with a faster growth rate, as in the genus *Coregonus* (Hile, 1937).

BIOLOGICAL CHARACTERS.—Biological characteristics that appear to be influenced by water temperature include minimum size at maturity, maximum size, maximum age, fecundity, and spawning times. Female *tyrannus* become sexually active at a smaller size in the southern Atlantic area than in the middle Atlantic area (Higham and Nicholson, 1964) of the United States coast. The minimum and mean fork lengths of sexually active specimens were 210 mm and 225 mm respectively in the middle Atlantic area, and 180 and 203 respectively in the southern Atlantic area. The smallest active females were age 1 in both areas. Not enough mature *patronus* are available for comparison. An earlier maturation would partially account for the smaller size of *patronus* as the onset of sexual maturity inhibits growth in fishes (Brown, 1957).

The maximum size of *tyrannus* is about 500 mm total length or 400 mm standard length (Hildebrand, 1963; Cooper, 1965). The largest specimen of *patronus* I found was 232mm standard length and from the gulf coast of Florida. *B. patronus* apparently is smaller than *tyrannus* at all stages of development from embryo to adult (Reintjes and Pacheco, 1966).

B. tyrannus may live a maximum of 10 years (June and Roithmayr, 1960). In the 1964-65 gulf fishery most *patronus* were 1 or 2 years old, and less than 1 per cent were from 4 to 6 years old (Chapoton, 1967). Scales of all the larger specimens I examined from the gulf coast of Florida had fewer than five annuli. Reintjes (1964a) noted a nearly complete mortality of *patronus* at age 3. Migration as an explanation is unlikely because an older stock has not been discovered. *B. tyrannus* in the South Atlantic fishery (Warlen, 1967) is similar in age composition to *patronus* (Chapoton, 1967). I collected much larger specimens of *tyrannus* (to 325 mm standard length) from the Indian River of Florida.

Fecundity is related to body size and, therefore, to water temperature. McHugh (1951) demonstrated that a decrease in fecundity to the south was related to body size in the northern anchovy (*Engraulis mordax*). *B. tyrannus* produce from 38,000 to 631,000 ova each season (Higham and Nicholson, 1964). *B. patronus* has a lower mean fecundity, 21,960 to 122,062 (Suttkus and Sundararaj, 1961), but according to Higham and Nicholson (1964) a higher mean fecundity when specimens of equal length are compared.

The *tyrannus* spawning season is clearly limited over its geographic range to a maximum mean monthly water temperature of about 70°F, although minimum and average spawning temperatures do increase to the south (Table 15). A similar maximum holds for all forms found along the Florida coasts. High water temperatures probably limit spawning of menhadens in the vicinity of Key West and Miami Beach, where minimum monthly means are 71.3 and 70.6 respectively (U. S. Coast and Geodetic Survey, 1960).

It may be significant that *tyrannus* spawned when water temperatures were both rising and falling, whereas *smithi* spawned only when temperatures were rising.

Menhaden Populations

My taxonomic conclusions are based primarily on degree of divergence of morphological characters, although biological characters and probable evolutionary history are also taken into consideration. Four species are recognized from the Atlantic and gulf coasts. Seven distinct forms of menhadens are found on the Florida coasts: *patronus,* two races of *tyrannus,* two races of *smithi,* and two hybrid combinations (Figure 3).

Populations of large-scaled menhaden.—Menhaden forms are examples of Atlantic and gulf cognates for which levels of divergence up to the species level have been recognized. Discontinuity of samples in southern Florida often makes it difficult to determine if cognates represent: 1) a single continuous population, possibly with subpopulations in the Atlantic and Gulf of Mexico; 2) two allopatric populations that may or may not have diverged; 3) two populations that are sympatric in southern Florida. A change in nomenclature should be based on proof, or at least strong evidence, rather than a controversial opinion. The gulf and Atlantic forms of large-scaled menhadens should be relegated to subspecies if it can be demonstrated that 1) they represent a single continuous population; 2) obvious intergradation exists between Atlantic and gulf populations, even if they are primarily allopatric; 3) morphological and biological differences are minor; or 4) major differences are not genetically based.

The large-scaled menhadens (*tyrannus* and *patronus*) appear to be allopatric, with a hiatus on the Florida Atlantic coast between West Palm Beach and the Florida Keys (Figure 3). Three meristic characters are highly divergent between the two populations and consistent over their ranges, indicating little or no intergradation. Divergent characters (Table 22) include gill filaments on ceratobranchial arch (95% divergence), ventral scutes (93%), predorsal scales (90%), and vertebrae (92%, if all specimens are considered;

85%, if only Indian River *tyrannus* is compared to *patronus*) (Tables 6, 7, 9, 18). Lower levels of divergence are obtained for pectoral rays (78%), body depth (83%), head depth (81%), dorsal rays, pectoral fin length, anal fin base length, and dorsal fin base length (Tables 22, 23). No significant difference is found for lateral scale rows, anal rays, opercular striations, head length, upper jaw length, mandible length, and caudal peduncle depth (Tables 22, 23). Divergences of vertebral count (Table 7) and proportions were calculated by comparing *patronus* to the Indian River sample of *tyrannus* partially to take into account geographic variation of these characters in *tyrannus*. The character of gill filament number on the ceratobranchial arch (Table 9), although not used previously, is nevertheless consistent. Biological differences between the two large-scaled cognates such as maximum size, maximum age, and fecundity indicate these forms are isolated. Determination of the taxonomic status of these two forms is complicated by the introgressive hybridization with *smithi* on the Florida coast.

The similarity of the Atlantic hybrid *smithi* x *tyrannus* to the gulf hybrid *smithi* x *patronus* suggests that genetic differences between *tyrannus* and *patronus* are minor. The greatest difference appears to be the usual presence of a lower row of spots in the gulf hybrid which is usually absent in the Atlantic hybrid (Figures 1 and 2). Since the other parent, *smithi*, is divergent only to a racial level, it could not impart major differences to the two hybrids. However this comparison of hybrids is not a valid genetic test because all progeny analyzed are not F_1 hybrids.

The population structure and migration patterns of *tyrannus* have not been fully described. An analysis of four meristic characters reveals two populations of juveniles, one occurring north of Long Island and one to the south (June, 1958). Numbers of vertebrae, scutes, dorsal rays, and left pectoral rays decrease to the north (June, 1958). An extensive study of vertebrae verified these results (Sutherland, 1963), and I found the same trend with scutes and pectoral rays using different specimens. June (1965) found that spring spawners occurring between Cape Cod and Long Island have lower vertebral numbers than autumn spawners occurring between Long Island and North Carolina. Spawners and nonspawners form large schools in October and migrate south in November. Spawners congregate off North Carolina until mid-December (June, 1965), then disappear.

June (1958) found homogeneity of four meristic characters (vertebrae, scutes, pectoral rays, dorsal rays) in *tyrannus* from Long Island,

N. Y., to Georgia. Significant differences in three proportions (pectoral fin length, anal fin base length, caudal peduncle depth) (Table 24) between the Chesapeake Bay and North Carolina samples, and uniformity of the North Carolina and Fernandina Beach samples (Tables 22, 24) provide evidence for a southern Atlantic area population ranging from North Carolina to northeastern Florida. Southern Atlantic menhadens are of much smaller average size in the summer commercial fishery than in all fisheries to the north (Nicholson and Higham, 1965).

A distinct race of *tyrannus* occurs in the Indian River area of Florida, probably ranging from near Cape Kennedy to Jupiter Inlet. June (1958) found this species to be uniform in vertebral count between New York and Georgia. The Indian River population has a significantly lower number of vertebrae (Table 7) and is distinct from the Fernandina Beach and more northern samples in seven proportions (body depth, head length, head depth, maxillary length, mandible length, pectoral fin length, and anal fin base length) (Table 24).

Characteristics of *patronus* are fairly homogeneous along the gulf coast, but specimens from the Horseshoe Beach and Suwannee areas are generally larger and darker than northern gulf specimens. Certain characteristics of the eight adults from Sarasota Bay appear to grade into the hybrid's characteristics.

Several patterns of variations are found in proportions of the large-scaled manhadens (Tables 23 and 24). Characters that produce a continuous cline (apparently correlated with water temperature) in *tyrannus* and *patronus* include body depth, dorsal fin base length, caudal peduncle depth, and pelvic fin shape. Proportions that appear to be homogeneous in the Atlantic (with the exception of the Indian River population, in which they are shorter) include head depth and lengths of head, maxillary, and mandible. The short head is typical of the Indian River population, but longer-headed fish also occur there; both forms are shown in Figure 1. The head of *patronus* is short, but deeper than typical Indian River *tyrannus*. Pectoral fin length increases to the south with the exception of the Indian River population. The inner and middle rays of the pelvic fin increase relative to the outer rays, to the south in *tyrannus* and *patronus* (Table 4, Fig. 5).

Proportions that are greater in *patronus* than in Indian River *tyrannus* include body depth, head depth, pectoral fin length, anal fin base length, and dorsal fin base length.

Hildebrand (1948) neither presented data on geographic variation nor gave the size of specimens used. He noted that several proportions increase to the south in *tyrannus* (head depth, lengths of head, maxillary, mandible, pectoral fin, and caudal fin). My data do not in general support his conclusions. I did not examine caudal fin length.

The nominal species *B. brevicaudata* Hildebrand, known only from type specimens from Noank, Connecticut, Berry (1964) regarded as a form of *tyrannus* that was "malformed by environmental stress". The distinctive shortened proportions (depth of head, lengths of head, maxillary, mandible, pectoral fin, caudal fin) probably resulted from a water temperature extreme during development. The specimens are not hybrids.

POPULATIONS OF SMALL-SCALED MENHADENS.—*B. smithi* Hildebrand was described in 1941 from North Carolina. *B. gunteri,* described by Hildebrand (1948) from Texas coast specimens, was thought to be the gulf cognate of *smithi.* Hildebrand's posthumous paper (1963) correctly characterized this eastern gulf population as intermediate between *gunteri* and Atlantic *smithi,* but nearer to the latter. Christmas and Gunter (1960) compared 25 *smithi* collected off eastern Louisiana, Mississippi, and Alabama to 30 *gunteri* from Louisiana in three meristic characters (vertebrae, ventral scutes, predorsal scales) and three proportional characters (head length, head depth, pectoral fin length). They considered *gunteri* to be a distinct species and observed that both species were collected in Chandeleur Sound, Louisiana. I have used their data on vertebral counts. My samples include the same specimens of *gunteri* from Louisiana and the only two specimens of *smithi* that are still available from the Mississippi Delta area.

B. gunteri and *smithi* are valid species because they are highly divergent, and available specimens do not intergrade. High levels of divergence between *smithi* and *gunteri* are obtained with vertebrae (99% divergence), mandible length (100%), upper jaw length (98%), head length (98%), head depth (92%), and ventral scutes (85%) (Tables 22, 23). The number of scale rows between the tip of the pectoral fin and base of pelvic fin is usually one or two in *gunteri* and usually three to five in *smithi.* Significant differences between the two gulf species are obtained with lateral scale rows, anal rays, opercular striations, pectoral fin length, and anal fin base length (Tables 22, 23). *B. gunteri* usually has a higher number of gill rakers (Fig. 8) than the gulf population of *smithi.* As a result of

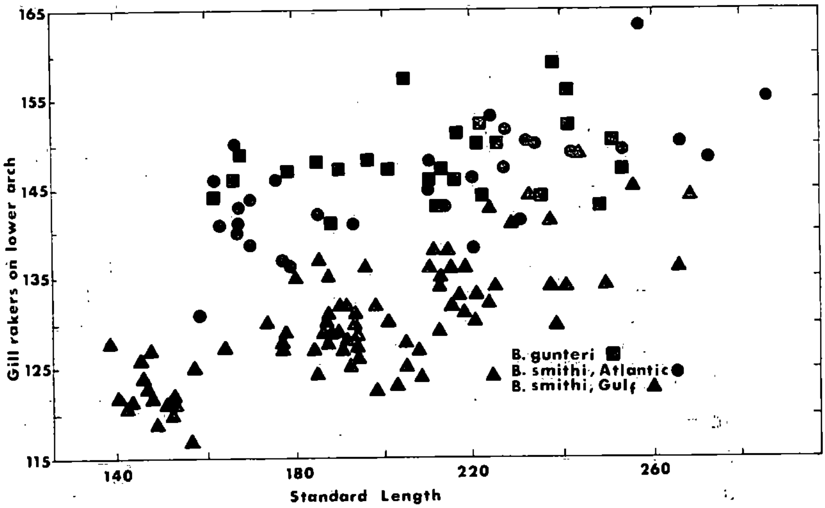


FIGURE 8. Relationship of gill raker numbers to standard length in *Brevoortia smithi* from Atlantic Ocean, *smithi* from eastern Gulf of Mexico and *gunteri* from western gulf.

convergence, as discussed previously, *gunteri* is similar to the Atlantic population of *smithi* in gill raker count. No difference between these two species from the Gulf of Mexico is apparent with other characters (predorsal scales, gill filaments, dorsal rays, pectoral rays, dorsal fin length, caudal peduncle depth, body depth).

B. smithi is represented by two populations, one in the Atlantic Ocean ranging from North Carolina to Jupiter Inlet, Florida, and another in the Gulf of Mexico ranging from Florida Bay to Chandeleur Sound, Louisiana (Fig. 3). A significant difference occurs between the Indian River sample of the Atlantic population and the Florida Bay sample of the gulf population in predorsal scales, vertebrae, ventral scutes, and gill filaments (Table 22). Lateral scale rows are highly variable but means are lower in the gulf population (Table 8). Gill rakers are lower in the gulf samples (Tampa Bay and the Apalachicola area) than in the Indian River sample (Fig. 8).

MENHADEN ZOOGEORAPHY

The emergence of the Florida plateau and subsequent invasion of the shallow-water zone by both tropical and temperate-water fishes resulted in an ecological situation highly suitable for speciation in marine fishes. Long continued environmental fluctuations along the Florida plateau and in the northern Gulf of Mexico favored the occurrence of wide-ranging adaptable species (Hedgpeth, 1954). Evolutionary responses of inshore fishes to the emerged Florida plateau include (1) extension of ranges along the Florida coasts, (2) speciation in new niches, (3) divergence of Atlantic and gulf cognates, and (4) hybridization. Ginsburg (1952) believed that the southern limit of the temperate Atlantic fauna is between Cape Kennedy and Biscayne Bay, Florida. Many temperate-water species are abundant south of Cape Kennedy in the Indian River area. For example, the two species of menhadens and their hybrid in the Atlantic are common south to the connected Indian River and Jupiter Inlet lagoons. They were not reported farther south in studies by Christensen (unpublished master's thesis) or Springer and McErlean (1962). Two specimens of *smithi* recently collected near Miami (Frederick H. Berry, pers. comm.) were probably stragglers.

Extensive evolutionary radiation resulted in a large number of endemic species in Florida waters. Briggs (1958) recognized 85 endemic species including 63 shore species. Menhaden forms in the area increased from two to seven (including hybrids) as a result of the emergence of the Florida plateau.

The emergent Florida plateau is a physical barrier, and its southern tropical environment is an ecological barrier, to the distribution of temperate-water marine fishes (Ginsburg, 1952; Briggs, 1958; Hildebrand, 1963). The emergent plateau separated continuous populations of large-scaled and small-scaled menhadens into Atlantic and gulf cognates, which subsequently diverged. Meristic characters, which are highly divergent between the two large-scaled menhaden species and highly consistent within each form, probably were clinal before trans-Florida isolation occurred. With isolation, meristic characters apparently became less clinal although proportional characters remained strongly clinal.

Many temperate marine fishes are discontinuous in southern Florida. Some that show temperature-related movements include the spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogon undulatus*). These two species occurred in Florida Bay only after the extremely cold winter of 1957-1958 (Tabb and Manning, 1961), but some spot remained through warmer months. Silver perch (*Bairdiella chrysura*) and pigfish (*Orthopristis chrysopterus*), primarily inhabitants of warm-temperate water, became common in the tropical Miami area only after the severe winter of 1957-58 (Springer and Woodburn, 1960).

Segregation of gulf and Atlantic populations has been demonstrated by tagging experiments. Of returns of *Cynoscion nebulosus* tagged on the Florida gulf coast, 95 per cent were captured within 30 miles, 5 per cent moved up to 315 miles and none was recovered in the Everglades National Park or in the Atlantic (Moffett, 1961). Of returns of *Mugil cephalus* tagged on the Florida gulf coast, 91 per cent were recovered within 20 miles, 9 per cent moved up to 350 miles, and none was recovered in the Atlantic (Broadhead and Mefford, 1956). No trans-Florida movement of temperate-water fishes was observed in tagging studies by Moe (1966) and Topp (1963). A "disjunct pattern", discontinuity in southern Florida, was noted for 65 species of invertebrates (Hedgpeth, 1954). Yet trans-Florida migration does occur in some tropical or migratory species including the shark *Carcharhinus milberti* (Springer, 1960).

Considerable geological time would be required for isolated gulf and Atlantic cognates to diverge to a species level. Cooke and Mossom (1929), Cooke (1939), and MacNeil (1950) considered the "Pleistocene terraces" of Florida to be related to Pleistocene transgressions. Recent dating of terrace deposits by Alt and Brooks (1965) and Tanner (1965) indicated that the highest Florida terraces (215-250 feet) are Miocene, possibly Oligocene; intermediate terraces (30-120 feet) are Pliocene; and lower terraces (0-30 feet) are Pleistocene. The Florida plateau emerged above sea level as early as the Miocene or Oligocene but it was not continuously effective in isolating gulf and Atlantic populations as the plateau was partially submerged several times during interglacial periods. Also temperatures were cool enough in the Pleistocene to permit movement of temperate water species between the gulf and Atlantic without total submergence of the Florida plateau (Hedgpeth, 1954). During the last glacial period the temperate shore fauna was displaced southward, according to Walters and Robins (1961), to what is now the northern West Indies. The discontinuous gulf and Atlantic cognates have thus been continuously isolated only since the recession of the Wisconsin glacier, which probably terminated about 10,000 years ago. Considerable divergence could have occurred before that time as a result of clinal variation and periodic isolation of cognates by the Florida peninsula during each glacial cycle.

The emergence of the Florida plateau provided an additional optimum habitat (warm-temperate coast) for small-scaled menhadens near the northern fringe of their previous distribution. Divergence of *smithi* and *gunteri* resulted from some kind of barrier in the northern gulf. East and west Gulf of Mexico cognates are found in other fishes including *Gymnachirus* (Dawson, 1964), *Hippocampus* (Ginsburg, 1952), and *Archosargus* (Caldwell, 1965). As the western forms of *Archosargus* and *Gymnachirus* range to east of the Mississippi River Delta, the river or its delta do not currently produce an effective barrier. Baughman (1950) believed that the fauna of the east and west gulf were cut off by the "vast and silt-laden flood" of the Mississippi. Ginsburg (1952) agreed with Baughman but also considered a hypothetical peninsular barrier extending out from the Florida panhandle and Alabama. The restriction of a "large percentage" of 108 gulf species to the northeastern gulf is related to the presence of a coral community that extends to near the western boundary of Florida (Briggs, 1958), but *smithi* is not associated with the coral community.

Glacial cycles could also account for east and west Gulf of Mexico cognates. Cooling of the coastal waters by one or more of the major Pleistocene glaciers could have forced the small-scaled menhadens to the south, resulting in discontinuity across the northern Gulf of Mexico. Divergence probably occurred during earlier glaciations as later cycles were shorter (Neill, 1957). With warming of the coastal waters the two species of small-scaled menhadens would have become sympatric on the central gulf coast. The few specimens available from the area of sympatry do not indicate hybridization of these closely related species. The apparent scarcity of these species where they are sympatric is in contrast to the abundance of the parental forms, favoring hybridization, on the Florida coasts. Limited spawning of small-scaled menhadens in the northern Gulf of Mexico is suggested by the absence in collections of juveniles from Matagorda, Texas, to Tampa Bay, Florida, according to Reintjes and Pacheco (1966). However Suttkus (1958) reported juvenile *smithi* from Cedar Keys, Florida, but not from farther north.

If large-scaled forms diverged in the east and west Gulf of Mexico, the populations subsequently fused. *B. patronus* was less likely to become discontinuous than small-scaled menhadens because it is adapted to colder waters and is more migratory. Whereas cold coastal water was the barrier to east and west gulf cognates during glacial periods, warm tropical water was the barrier to Atlantic and gulf cognates during the interglacial periods.

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