FISHES INHABITING THE OUTER BANKS OFF NORTH CAROLINA: THEIR ORIGIN AND DISPERSAL

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With 2 figures and 2 tables

ABSTRACT. Historical origins, type, and movement of North Carolina's Outer Banks isolated islands and oceanography are reviewed. Fishes inhabiting freshwater ponds located on the islands are compared in relation to species origin, presence on each island, their dispersal within the Outer Banks system, and relationships between islands. Eighteen species frequent the island ponds as follows: Hatteras 12 ponds, 7 species; Ocracoke 2, 7; Portsmouth 33, 13; Core Banks 41, 7; and Shackleford Banks 18, 10. Ocean and lagoonal habitats are also examined as possible sources of the fishes inhabiting the islands. Historical changes in the fish fauna of Mullet Pond (Shackleford Banks) is noted as an example, in the light of constantly natural and man-made changes in island ecologies, of the possible fate of each island's pond fishes.

INTRODUCTION

Most islands located in the Atlantic Ocean are of volcanic origin, exist atop sea mounts, and possess short rivers or no inland standing waters (EDWARDS 1990; PENRITH 1967). Inshore or inland fish faunas of such islands may be endemic, related to nearby continents or a result of continental drift and ocean currents to or from mainland regions (BÖHLKE & CHAPLIN 1968; DIETZ & SCROLL 1970; DOOLEY *et al.* 1985; GON & HEEMSTRA 1990; STERRER 1986). Rarely have marine and freshwater fish faunas of isolated western Atlantic Ocean islands, formed by accretion or frontal progression processes, been examined (LEATHERMAN 1979; MOSLOW & HERON 1979, 1981; OTVOS 1985; PIERCE 1969; PIERCE & COLQUHOUN 1970; SHABICA *et al.* 1983).

This study documents the fishes inhabiting freshwater ponds located on North Carolina's isolated "Outer Banks" continental islands. I also review the origin of the islands, examine dispersal and the relationships between/and adjacent island fish faunas. The possible oceanic and inshore sources of the fishes inhabiting the ponds are discussed. Other factors that affect the islands' ponds and fish faunas are also included.

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STUDY AREA

The "Outer Bank" islands (DOLAN & LINS 1986) off North Carolina (Hatteras, Ocracoke, Portsmouth Islands, Core Banks, and Shackleford Banks) are the farthest projecting island land masses in the western North Atlantic Ocean. Origin and positioning of the islands have been controversial. The origin probably occurred sometime between the Pleistocene and Holocene. MOSLOW & HERON (1979, 1981) believed the islands were formed over a sand-fill base. PIERCE (1969) and PIERCE & COLQUHOUN (1970) believed that the northern islands were areas built upon material of mainland origin exposed to weathering; while they believed that southern islands were secondary barriers built upon marine sediments. Longshore sand movement southward along Hatteras Island and westward of Cape Hatteras is moving to isolate Shackleford Banks (Fig. 1, lower left corner) and move the entire barrier system and island westward. PIERCE & COLQUHOUN (1970) also established that barrier island system origin and movement was eastward into the Atlantic prior to subsequent movement westward to present island locations. Several East-West barriers have also formed during a progression of spit elongation southward at the rate of 45-98 m/century (MOSLOW & HERON 1979) and landward 1.6-3.6 km during the last 4,000 years (PIERCE & COLQUHOUN 1970). Cape Lookout (Fig. 1) once stood 3-5 km seaward of its present position and Cape Lookout, during the Pleistocene, was situated 25 km NW of its present location (PIERCE & COLQUHOUN 1970).

The present islands were also formed or shaped by 18, of 25 known, inlets. These inlets were once cut across the original barrier, following hurricane or northeast or northwest wind-wave storms, and/or caused overwash of the barrier islands (STICK 1958). Many areas along the present Outer Bank islands are barely above sea level (3 m is usual height, highest is 14 m at Cape Lookout). Maximum island widths range 0.8-2 km (widest 4 km at Cape Hatteras).

Seaward of the islands the ocean shelf is narrow (10 km off Cape Hatteras), increasing southward to 80 km off Cape Lookout and Shackleford Banks. The Gulf Stream off Cape Hatteras varies between 1-3 km offshore during the summer and 5-15 km during the winter, whereas off Cape Lookout, subject to seasonal winds, it varies between 15-20 km during the summer and 80-100 km during the winter. Shelf substrate at inlets is sandy, mixing with sand or mud along the beaches, changing to sand with increasing depth offshore.

Coastal ocean waters are turbid out to 15 m depths as a result of strong seasonal storm winds and waters pouring out inlets from the Pamlico-Albemarle lagoon that are carried by longshore currents outward. Salinities in these turbid coastal waters are usually 30-32 ppt. Waters seaward of 15 m are green and salinities are 32-34 ppt. Edge of shelf waters are blue, depths are 735 m, and salinities are 34-36 ppt. Southeast or southwest winds, during nine months of the year, influence tide height and sea state and deflect the Gulf Stream shoreward. Whereas, northeast or northwest winter winds for 3-4 months cause rough seas and extra high tides, resulting in extensive beach erosion around each island.

A vast lagoonal system composed of Pamlico and Albemarle Sounds (Fig. 1) extends in a north-south direction for 50-130 km and separates the islands from the mainland to the west. Lagoonal depths range to 7.3 m while most average 5 m. Salinities vary seasonally 0-30 ppt, highest in November and lowest in April following spring rains (SCHWARTZ & CHESTNUT 1973). Strong southwest summer or North-East and northwest winter winds cause turbid year-round lagoonal waters. This mixing condition enhances the status of the lagoon as a nursery area for shrimp, blue crabs, and fishes (ROSS & EPPERLY 1985; WOLFF 1976). The western portion of the lagoon has a muddy substrate, while near the islands it is sandy.

SAMPLING

A host of collections of the ocean waters adjacent to the Outer Banks islands of Hatteras, Ocracoke, Portsmouth, Core Banks, and Shackleford Banks (Fig. 1) have been carried out by state, federal, university, private sources, and the author. SCHWARTZ (1989) summarized the fishes collected by species, habitat, and province origin and noted 685 species inhabiting the ocean to depths of 600 m. Similarly a vast array of samples has characterized the fishes found in the landward Pamlico-Albemarle lagoon (EPPERLY 1984; ROSS & EPPERLY 1985; WOLFF 1976). WOLFF (1976) found 101 marine species frequenting the lagoonal sides of each Outer Bank island.

Ocean and lagoon water sampling was accomplished by using various sized otter trawls (19 mm mesh, 12 m wide), haul seines (15 cm mesh), and pound nets (19 mm mesh) (lagoon waters only). Trawl tows varied in direction and depth sampled.

Seine sampling of the 106 freshwater ponds scattered on Hatteras, Ocracoke, Portsmouth Islands, Core Banks, and Shackleford Banks found they contained a mixture of freshwater and marine origin fishes. Pond distribution was Hatteras 12, Ocracoke 2, Portsmouth 33, 41 throughout Core Banks, Shackleford Banks 18. Knotless nylon seines 3 mm meshed 1.2 x 3 or 1.2 x 7.5 m lengths were employed during oceanside and lagoon beach sampling. One to several seine passes were made in each freshwater island pond until no new species were encountered. Water and air temperatures, salinity, substrate composition, water depth and color, and oxygen content were also noted. All fishes were measured to nearest 0.1 mm standard length, weighed to 0.1 g, preserved in 10% formalin, later 10% isopropyl alcohol, and deposited in the curated Institute of Marine Sciences fish collection at Morehead City, NC. Freshwater was defined as having a 0-0.05 ppt salinity following the convention of the Venis Commission (1958).

RESULTS

While 188 freshwater ponds are located and sampled through-out the Outer Banks from Virginia to Beaufort Inlet, North Carolina (280 km), only 106 occurred on the isolated study islands (SCHWARTZ 1992). Twenty-nine species of fishes were collected through-out the Outer Banks, 25 of which occurred in mainland ponds from Virginia to the treacherous Oregon Inlet (Fig. 1, Table 1). Eighteen species frequented the island ponds as follows: Hatteras 12 ponds, 7 species; Ocracoke 2, 7; Portsmouth 33, 13; Core Banks 41, 7; and 18, 10 on Shackleford Banks (Table 1). Numbers and weights of the combined catches/island reviewed from north to south were: Hatteras 481 fish (281.5 g weight), Ocracoke 316 (587.4 g), Portsmouth 5,447 (6,237 g), Core Banks 1,163 (1,018.2 g), and Shackleford Banks 4,521 (5,126.8 g), for a total of 11,928 specimens weighing 13,250.7 g.

SCHWARTZ (1989) noted 685 species frequented ocean waters surrounding the islands, 196 in oceanic waters adjacent to each island beach, 116 in lagoon waters (96 were common to both bodies of waters). WOLFF (1976) sampling the lagoonal side of each island collected 106 marine and freshwater fishes. Entry of oceanic fishes into the lagoon was via the numerous inlets: Oregon, Hatteras, Ocracoke, Haulover, Drum, Barden, and Beaufort (Fig. 1).

Of the fishes inhabiting ponds on Hatteras, Ocracoke, Portsmouth Islands, Core Banks, and Shackleford Banks, 14 were found in the Pamlico lagoon while five were of high saline ocean water derivation (Fig. 1). Four of the 18 species inhabiting the study islands were primary freshwater fishes (MYERS 1938) such as: carp, *Cyprinus carpio* LINNAEUS, 1758, and three sunfishes, pumpkinseed, *Lepomis gibbosus* (LINNAEUS, 1758), bluegill *Lepomis macrochirus* RAFINESQUE, 1819, and largemouth bass, *Micropterus salmoides* (LACEPÈDE, 1802) (Table 1). Fourteen were secondary fishes (marine fishes that can adapt to freshwater existence) that inhabit marine waters but can adapt to freshwater (MYERS 1938). As one progresses southward through the islands, pond substrates changed from muddy to sandy on Ocracoke, Portsmouth Islands, Core and Shackleford Banks. Likewise, Hatteras Island from Buxton to Oregon Inlet, Ocracoke, and Portsmouth-Core Banks were subject to frequent ocean overwash, a process that added or replenished the fish faunas of each island's ponds, often annually. This process was vividly demonstrated in Mullet Pond, a pond near the western end of Shackleford Banks (Fig. 1), once 2.6 km, today 0.04 km in extent. Mullet Pond has had its marine oriented fish fauna changed or restricted over an 86 yr period by the waters changing from high salinities to freshwater (Schwartz 1970; Schwartz et al. 1990). Mullet Pond's fish fauna composition changed from 26 species in 1914 to a stable five in 1990: variegated minnow (*Cyprinodon variegatus*) LACEPÈDE 1803, marsh killifish (*Fundulus confluentus*) GOODE AND BEAN, 1879, mummichog (*Fundulus heteroclitus*) (LINNAEUS, 1766), rainwater fish (*Lucania parva*) (BAIRD AND GIRARD, 1855), and mosquitofish (*Gambusia holbrooki*) GIRARD, 1859.

South of Oregon Inlet, seven species of fishes (Fig. 2) have apparently been able to cross the treacherous inlet from the mainland to the north, five species have crossed Hatteras Inlet to inhabit Ocracoke Island while eight passed southward onto the Portsmouth-Core

Banks complex; only seven crossed Barden Inlet to inhabit Shackleford Banks (TABLE 1, Fig. 2). Seven of the fishes found on Hatteras Island also occur on the mainland to the north while only four occupy islands to the south (Fig. 2). Ocracoke Island's seven species relate as follows: Three are common with Hatteras Island to the north, six are similar to mainland species, while five are common with Portsmouth, Core and Shackleford Banks to the south (Fig. 2). Only five of the Portsmouth-Core Banks fishes are common with Ocracoke Island's fauna (to the north), three are similar to Hatteras Island's fauna, 10 are similar to those on Shackleford. Thus, Hatteras Inlet seems to be a barrier separating mainland origin fishes from those inhabiting islands south of the inlet. This can be further seen on examination of size clines of the mosquitofish and variegated minnows as fishes from southern islands are usually larger and heavier than those from northern areas of the banks (SCHWARTZ *et al.* 1990). Likewise, mainland variegated minnows (a species found throughout the Outer Banks islands, Table 1), possess a different morphology, reinforcing the conclusion that northern Outer Banks fishes were of mainland but southern specimens were of marine origin and not the mainland to the west (SCHWARTZ *et al.* 1990).

Thus isolated marine islands should not be neglected for their marine and inland fish faunas should be sampled as ways to learn more about island and its fish origin(s). While secondary fishes might be expected to dominate an island's fauna, they may shed light regarding island origin and eventual fate or both. The effects of natural changes, as in Mullet Pond on Shackleford Banks, can reveal an interesting interplay and effects of natural ecological and habitat changes caused by hurricanes, storms, and tides. Also, the effects of man, through pollution and construction, may have serious effects on an island's faunal long-term existence. In any event, man should try to protect these fragile island habitats at all costs.

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REFERENCES

BÖHLKE, J. E. & C.C.G. CHAPLIN:
1968. Fishes of the Bahamas and Adjacent Tropical Waters. Livingston Publ. Co., Philadelphia, PA. 771 p.

DIETZ, R. S. & W. P. SCROLL:
1970. East Canary Islands as a microcontinent within the Africa-North American continental drift fit. Nature 226:1043-1044.

DOLAN, R. & H. LINS:
1986. The Outer Banks of North Carolina. Prog. Pap. U.S. Geol. Surv. 1177-R. 47 p.

DOOLEY, J. K., J. VAN TASSELL, & A. BRITO:
1985. An annotated checklist of the shorefishes of the Canary Islands. Am. Mus. Novit. No. 2824. 49 p.

EDWARDS, A. J.:
1990. Fish and fisheries of Saint Helena Island. Univ. New Castle Upon Tyne, England. 152 p.

EPPERLY, S. P.:
1984. Fishes of the Pamlico-Albemarle Peninsula, North Carolina; area utilization and potential impacts. Spec. Sci. Rep. 42, N.C. Dept. Nat. Res. Div. Mar. Fish., Morehead City, NC. 129 p.

GON, O. & P. C. HEEMSTRA (EDS.):
1990. Fishes of the Southern Oceans. J. L. B. Smith Inst. Ichthyol., Grahamstown, So. Africa. 465 p.

LEATHERMAN, S. P.:
1979. Barrier Islands from the Gulf of St. Lawrence to the Gulf of Mexico. Academic Press, NY. 325 p.

MOSLOW, T. F. & S. D. HERON, JR.:
1979. Quarternary evolution of Core Banks, North Carolina: Cape Lookout to New Drum Inlet. p. 211-236 in S. P. Leatherman (ed.), Barrier Islands, Academic Press, NY.

MOSLOW, T. F. & S. D. HERON, JR.:
1981. Holocene depositional history of a microtidal cuspate foreland cape: Cape Lookout, North Carolina. Mar. Geol. **41**:215-270.

MYERS, G. S.:
1938. The freshwater fishes and West Indian zoo-geography. Ann. Rept. Smiths. Inst. Publ. **3451**:339-364 for 1937.

OTVOS, E. G.:
1985. Barrier island genesis - questions of alternatives for the Appalachicola Coast, Northwestern Gulf of Mexico. J. Coastal Res. **1**(3):267-278.

PENRITH, M. J.:
1967. The fishes of Tristan da Cunha, Gough Island, and the Verma seamount. Ann. So. Afr. Mus. **48**(22): 523-548.

PIERCE, J. W.:
1969. Sediment budget along a barrier island chain. Sediment. Geol. 3:5-16.

PIERCE, J. W. & D. J. COLQUHOUN:
1970. Holocene evaluation of a portion of the North Carolina coast. Geol. Soc. Am. Bull. **81**: 3693-3714.

ROSS, S. W. & S. P. EPPERLY:
1985. Utilization of shallow estuarine nursery areas by fishes in Pamlico Sound and adjacent tributaries of North Carolina. pp. 207-232. Chp. 10 in A. Yenez-Aranciba (ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an ecosystem investigation. DR(R) UNAM Press, Mexico.

SCHWARTZ, F. J.:
1970. Fishes and changing ecology of Mullet Pond, a barrier island pond on Shackleford Banks, North Carolina. J. Elisha Mitchell Sci. Soc. **86**(1):31-34.

SCHWARTZ, F. J.:
1989. Zoogeography and ecology of fishes inhabiting North Carolina's marine waters to depths of 600 meters. p. 333-370 in Carolina Coastal Oceanography, R. Y George and A. W. Hulbert (eds.). NOAA-NURP Res. Rep. **89-2**.

SCHWARTZ, F. J.:

1992. Fishes and ecology of freshwater ponds on North Carolina's Outer Banks. p. 93-118 in Barrier Island Ecology of the Mid-Atlantic Coast: A Symposium. Tech. Rept. NPS/SER CAHA/NRTR-93/04, C. Cole and K. Turner (eds.).

SCHWARTZ, F. J. & A. F. CHESTNUT:

1973. Hydrographic Atlas of North Carolina's Estuarine and Sound Waters. UNC Sea Grant **S2-73-12**. 132 p.

SCHWARTZ, F. J., G. SAFRIT, C. JENSEN, & J. PURIFOY:

1990. Stability and persistence of the fishes inhabiting Mullet Pond, Shackleford Banks, North Carolina 1908-1989. J. Elisha Mitchell Sci. Soc. **106**(2):38-50.

SHABICA, S. V., N. B. COFER, & E. W. CAKE, JR. (EDS.):

1983. Proceedings of the Northern Gulf of Mexico Estuaries and Barrier Islands Research Conference, 13-14 June 1983, Biloxi, MS. U.S. Dept. Nat. Res. Park Serv. SE Reg. Off., Atlanta, GA. 191 p.

STERRER, W. (ED.):

1986. Marine Flora and Fauna of Bermuda, A Systematic Guide to the Identification of Marine Organisms. J. Wiley & Co., NY. 742 p.

STICK, D.:

1958. The North Carolina Outer Banks. Univ. N.C. Press, Chapel Hill, NC. 352 p.

VENIS:

Symposium on the Classification of Brackish Waters. 8-14 April 1958. Centro Naz. Studi Talasograf. Consigl. Naz. Richerche XI, Suppl. p. 5-248.

WOLFF, M.:

1976. Nursery Area Survey of the Outer Banks Region. U.S. Dept. Comm. NOAA-NMFS Project **2-222-R**, St. Petersburg, FL. 47 p.

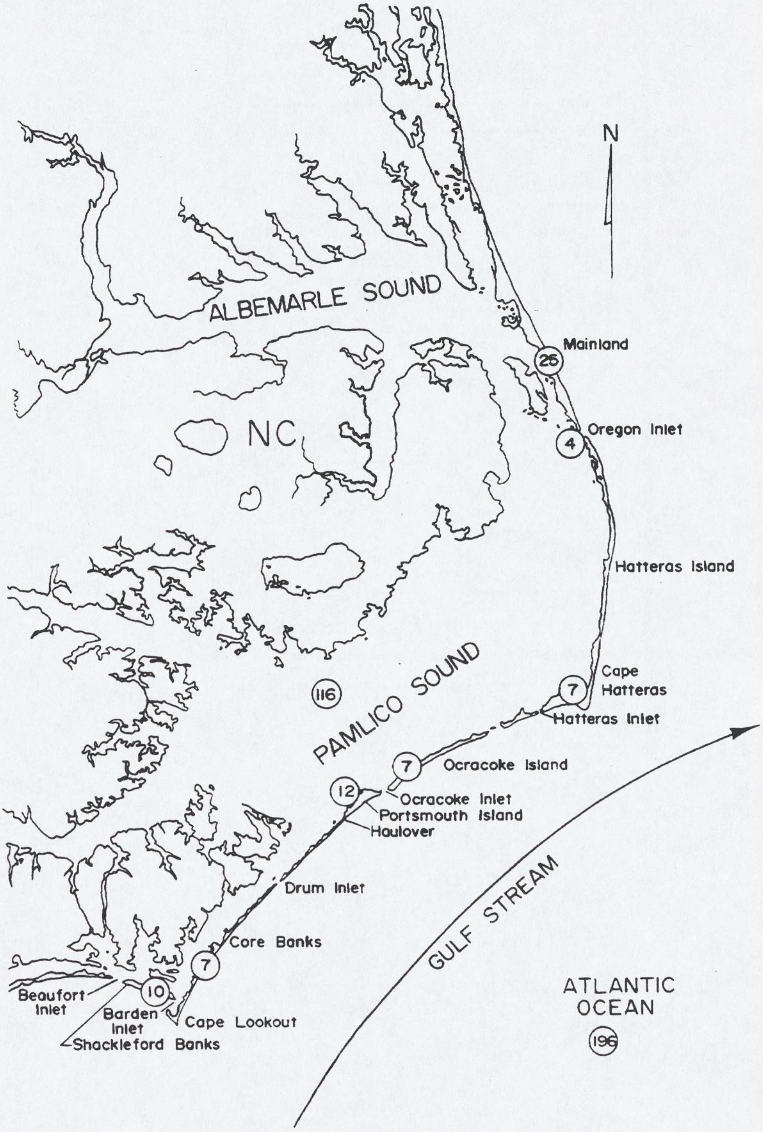

Figure 1 - Fishes, circled numbers, frequenting Outer Banks freshwater island ponds and surrounding lagoon or ocean waters.

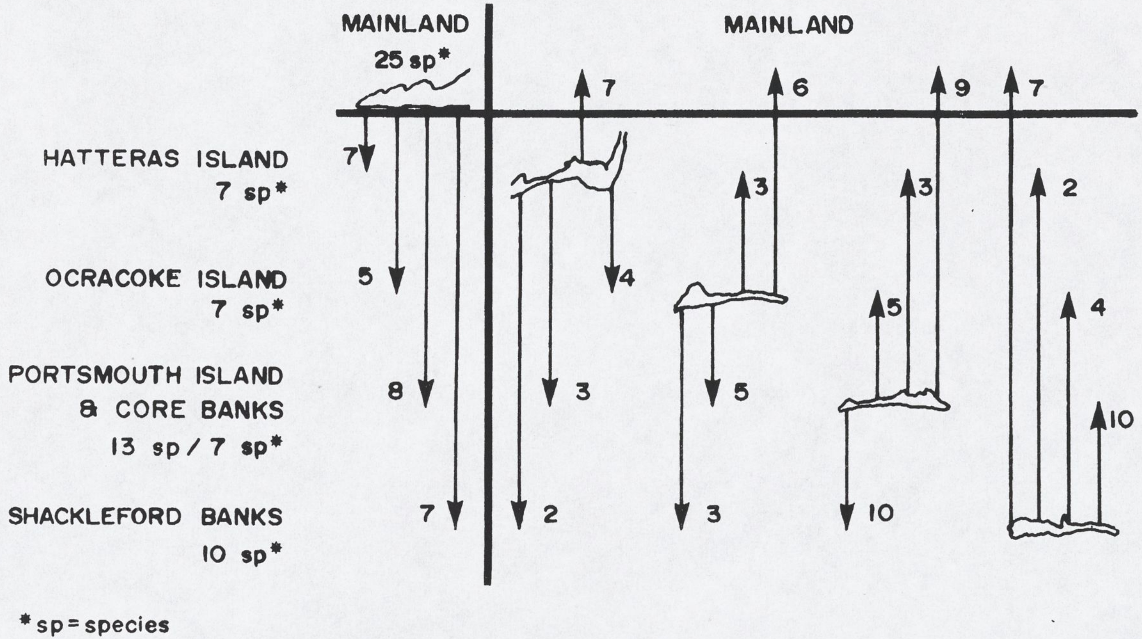

Figure 2 - Interrelationships of the species of fishes occurring on and between each North Carolina Outer Bank Island to that of the mainland.

TABLE I

Outer Banks pond regions, from north to South, frequented by each species captured by seine or trawl.

SPECIES	REGION					
	VA/ Oregon Inlet	Hatteras Island	Ocracoke Island	Portsmouth Island	Core Banks	Shackleford Banks
Gambusia holbrooki GIRARD, 1859	x	x	x	x	x	x
Lucania parva (BAIRD & GIRARD, 1855)	x	x	x	x	x	x
Cyprinodon variegatus LACEPÈDE, 1803	x		x	x	x	x
Anguilla rostrata (LESUEUR, 1817)	x	x	x	x		
Menidia beryllina (COPE, 1866)	x		x	x		
Fundulus confluentus GOODE & BEAN, 1879	x		x	x		
Fundulus heteroclitus (LINNAEUS, 1766)			x	x		
Mugil cephalus LINNAEUS, 1758	x			x		x
Leiostomus xanthurus LACEPÈDE, 1802	x			x		x
Elops saurus LINNAEUS, 1766	x		x			
Cyprinus carpio LINNAEUS, 1758	x	x				
Lepomis gibbosus (LINNAEUS, 1758)	x	x				
Lepomis macrochirus RAFINESQUE, 1819	x	x				
Micropterus salmoides (LACEPÈDE, 1802)	x	x				
Centrarchus macropterus (LACEPÈDE, 1801)	x					
Enneacanthus gloriosus (HOLBROOK, 1855)	x					
Lepomis auritus (LINNAEUS, 1758)	x					
Pomoxis nigromaculatus (LESUEUR, 1829)	x					
Fundulus diaphanus (LESUEUR, 1817)	x					
Morone americana (GMELIN, 1789)	x					
Ameiurus nebulosus (LESUEUR, 1819)	x					
Notemigonus crysoleucas (MITCHILL, 1814)	x					
Dorosoma cepedianum (LESUEUR, 1818)	x					
Lepisosteus osseus (LINNAEUS, 1758)	x					
Esox americanus GMELIN, 1788	x					
Fundulus luciae (BAIRD, 1855)				x		x
Fundulus majalis (WALBAUM, 1792)				x	x	x
Menidia menidia (LINNAEUS, 1766)				x	x	
Brevoortia tyrannus (LATROBE, 1802)						x

TABLE 2

List of 27 species of fishes known from Mullet Pond, Shackleford Banks, collected or reported by various researchers 1914-1989. Table from SCHWARTZ *et al*. 1990.

	Collectors										
	Hilde brand* 1914	Schwartz									
		Stras- burg*									
	16, 25, 30	1/07/59	6/08/69	30/05/76 6/06/76	21/04/82	12/04/84	21/05/85	3/06/87 30/06/87	30/06/88	6/5,3/6, 26/07/89	Total [5]
Elops saurus	√										
Brevoortia tyranus	√										
Opisthonema oglinum	√										
Anchoa eurystole [1]	√										
Anchoa hepsetus	√										
Opsanus tau	√										
Cyprinodon variegatus	√	422	77	64	356	260	68	223	288	206	1.964
Fundulus confluentus	√		11		10		289	291	53	44	698
Fundulus heteroclitus	√				53		3	209	3	12	280
Fundulus luciae [4]	√				1						1
Fundulus majalis	√										
Lucania parva [2, 3]	√	72	70	45	139	226	177	79	203	81	1.092
Gambusia holbrooki	√	125	513	374	692	183	319	252	382	129	2.969
Urophycis earlli	**										
Urophycis regia	√										
Menidia beryllina	√										
Menidia menidia	√										
Strongylura marina	√										
Mugil cephalus	√										
Mugil curema	√										
Echeneis naucrates	√										
Eucinostomus gula	√										
Ctenogobius stigmaticus	√										
Gobiosoma bosci	√										
Orthoprises chrysoptera	√										
Lagodon rhomboides	√										
Leiostomus: xanthurus	√										
TOTAL		619	671	483	1.251	669	856	1.054	929	472	7.004

* Unpublished.

** One about UNC 3050 was captured.

[1] Also recorded by RADCLIFFE (1914).

[2] Also recorded by KUNTZ (1916).

[3] Also recorded by TAGATZ and DUDLEY (1961).

[4] Also recorded by HILDEBRAND (1941).

[5] Total specimens collected only by SCHWARTZ 1969-1989.

18 May 1977

INTRODUCED FISHES IN NORTH AMERICA
(Established Species)

		States & Provinces
ANABANTIDAE		
Anabas testudineus (Bloch)	Climbing perch	FL[1]
Betta splendens Regan	Siamese fighting fish	FL
Ctenopoma nigropannosum (Reichenow)	Twospot climbing perch	FL[1]
CHARACIDAE		
Hoplias malabaricus (Bloch)	?	FL
CICHLIDAE		
Astronotus ocellatus (Agassiz)	Oscar	FL
Cichlasoma bimaculatum (Linnaeus)	Black acara	FL
Cichlasoma meeki (Brind)	Firemouth cichlid	AZ[1],FL
Cichlasoma nigrofasciatum (Günther)	Convict cichlid	AS,NV;ALB
Cichlasoma octofasciatum Regan	Jack Dempsey	FL[1]
Cichlasoma severum (Heckel)	Banded cichlid	NV
Cichlasoma trimaculatum (Günther)	Threespot cichlid	FL
Hemichromis bimaculatus Gill	Jewelfish	FL
Tilapia aurea (Steindachner)	Blue tilapia	FL,TX
Tilapia mariae Boulenger	Spotted tilapia	AZ[2],FL
Tilapia melanotheron (Rüppell)	Blackchin tilapia	FL
Tilapia mossambica (Peters)	Mozambique tilapia	AZ,FL
Tilapia zilli (Gervais)	?	AZ,FL[3]
CLARIIDAE		
Clarias batrachus (Linnaeus)	Walking catfish	FL
COBITIDAE		
Misgurnus anguillicaudatus (Cantor)	Oriental weatherfish	CA,MI
CYPRINIDAE		
Barbus tetrazona Bleeker	Tiger barb	CA
Carassius auratus (Linnaeus)	Goldfish	many
Ctenopharyngodon idella (Valenciennes)	Grass carp[4]	AR,AL,KY, IL,LA,MD

Cyprinus carpio Linnaeus	Carp	most
Leuciscus idus (Linnaeus)	Ide	CN
Rhodeus sericeus (Pallas)	Bitterling	NY
Scardinus erythrophthalamus (Linnaeus)	Rudd	NY
Tinca tinca (Linnaeus)	Tench	CN;BC - CO

ESOCIDAE

Esox reicherti Dybowski	Amur pike	NY[6],PA;ONT[6]

GOBIIDAE

Acanthogobius flavimanus (Temminck & Schlegel)	Yellowfin goby	CA
Tridentiger trigonocephalus (Gill)	Trident goby	CA

LORICARIIDAE

Hypostomus sp.	Armored catfish	FL[5]

POECILIIDAE

Belonesox belizanus Kner	Pike killifish	FL[1]
Poecilia hybrid	Lyretail black molly	FL[1]
Poecilia latipunctata (Meek)	Broadspotted molly	FL[1]
Poecilia mexicana Steindachneri	Shortfin molly	AZ,NV
Poecilia petenensis (Günther)	Swordtail molly	FL[1]
Poecilia reticulata Peters	Guppy	FL,NV
Xiphophorus helleri Heckel	Green swordtail	AZ,FL;ALB
Xiphophorus maculatus (Günther)	Southern platyfish	FL,NV
Xiphophorus variatus (Meek)	Variable platyfish	AZ,CA,FL,MN
Xiphophorus maculatus x helleri	Red swordtail	FL[1]

SALMONIDAE

Salmo letnica (Karaman)	Ohrid trout	~~CO~~[6],WY[6]
Salmo trutta Linnaeus	Brown trout	many

[1]current status (= still established) unknown

[2]photo in Minckley's book appears to be of T. mariae, not T. nilotica

[3]possibly eradicated

[4]probably established as evidenced by commerical catches in Mississippi drainage or Arkansas has been far more generous than imagined

[5]probably more than one species established

[6]current status unknown on purposeful introduction

Prepared by WALTER R. COURTENAY, JR.

NOT FOR PUBLICATION

EFFECTS OF FRESHWATER RUNOFF ON FISHES OCCUPYING THE FRESHWATER AND ESTUARINE COASTAL WATERSHEDS OF NORTH CAROLINA

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Morehead City, North Carolina

ABSTRACT

Presently 37 freshwater and 77 marine fishes, within 13 freshwater and 38 marine families, respectively, are known to inhabit the oligohaline or euryhaline "freshwater" estuaries of coastal North Carolina for prolonged periods. Most species are typical primary, secondary, diadromous, complementary or sporadic fishes, as defined by Myers (1938; 1949a,b; 1951). Eighteen of the freshwater and 37 of the marine fishes noted are new additions to the lists compiled by Schwartz (1964) and Gunter (1942, 1956) of known fishes which occur in low salinity fresh waters. The extent of the euryhaline zone created by seasonal or sudden runoff conditions, is described for each of the major coastal watersheds of North Carolina. Maximum or minimum salinity occurrence levels are noted for each species frequenting the area. Comments similar to Gunter *et al*. (1974) are presented on length of survival in low saline water situations and/or responses to other environmental variables, in relation to fish size.

INTRODUCTION

Fishes are usually categorized as primary, secondary, peripheral freshwater or marine, yet we know that there are anadromous, catadromous, diadromous, amphidromous, potamodromous, oceanodromous, vicarious, complementary or sporadic (Myers 1938; 1949a, b; 1951) fishes that pass into or out of fresh or marine regimes (Hoar and Randall 1979). Faunal fish surveys, however, are usually stilted to sampling either in fresh or marine habitats (i.e., Carr and Goin 1955; Douglas 1974; Livingston *et al*. 1976, 1977). Occasionally, there have been efforts to study the "salting out" effects where fresh waters mix with marine waters (i.e., Chesapeake Research Consortium 1976; Lauff 1967; Wiley 1978). More importantly almost no prolonged study has been aimed at that unstable area where fresh waters meet estuarine waters, the area that was estuarine and which suddenly is transformed into a freshwater habitat by increased freshwater runoff or to what happens to the fish faunas of either regimes when subjected to sporadic or rapid freshwater intrusions.

DEFINITIONS AND TERMINOLOGIES

While some would prefer to call that area located between fresh and saline waters, where two waters dilute each other, an estuary (Hedgpeth 1951; McHugh 1966; Lauf 1967; Pritchard 1967a), others designate it as brackish waters (Dahl 1956; Kinne 1964; Caspers 1967). To others the battle rages on in the search for an adequate terminology that defines the freshwater-saline interzone (McHugh 1967; Abbott and Dawson 1975; Schubel and Hirschberg 1978). Some even characterize this body of water by inferring it is made up of monotonous or abundant, mainly euryhaline marine fishes (Hedgpeth 1957). I am likewise at a loss when referring to this stratified euryhaline zone or habitat which flood or freshwater runoff waters convert into a purely freshwater habitat (Pritchard 1967a). Is it simply an extension of the freshwater zone or should some new terminology be applied to this temporary zone, habitat, or condition?

The unsettled definition of what is fresh water (Gunter et al. 1974) rages just as that of what is an estuary. For many years fresh waters were defined as those of 0.2 to 0.05 percent (Valikanges 1933; Dahl 1956) even though an international attempt was made to classify fresh water as those of 0-0.5 ppt salinity (Symposium in Classification of Brackish Waters 1958). Kinne (1964, 1967) presented good overviews to the problem. Gunter et al. (1974) and Odum (1953) presented excellent reviews of the physiological and environmental influences on estuarine fishes which can be extended to what happens to a fish which finds itself suddenly "trapped" or subject to a runoff freshwater intrusion area of a stream or river. I will not resolve, herein, the question of whether such fishes should be referred to as euryhaline, oligohaline or some other designation (Gunter 1942, 1956; McHugh 1964; Gunter et al. 1974) but add to the list of known occurrences of fresh water and marine fishes that we know live in such waters, with comments on their sizes, and possibly interacting factors.

METHODS

The fishes encountered in the runoff zone of the major rivers of North Carolina were captured during the past 12 years (1968-1980) by various sized anchored gill nets and 8.0-13.5-m semiballoon otter trawls. Gill net sets were usually for 24 hr and trawl tows were for 0.25 to 0.5 hr duration. Specimens captured by gill net, unless too damaged by crabs or decayed by high summer water temperatures, or otter trawl were preserved in the field in 10 percent formalin for later study and/or inclusion in the fish collection at the Institute of Marine Sciences, Morehead City, North Carolina.

Environmental variables of water temperature, oxygen, current speed, tide state, salinity were recorded by Taylor temperature thermometers (°C), direct reading YSI oxygen (ppm)-temperature probes, and A/O refractometers for salinity in ppt. Fish lengths were recorded as standard lengths unless a total (tonguefish) or fork length (sturgeon) was more representative.

DESCRIPTION OF NORTH CAROLINA RIVERS AND SOUNDS

Schwartz and Chestnut (1973), Williams et al. (1973), and Williams and Deubler, in part (1968), compiled the seasonal isohalines of the sound and coastal waters of North Carolina. The rivers that empty into the coastal sounds (Figure 1) are most affected in early spring, especially March or April, when runoff (the result of rains or melting snow upstream) is highest. The major watersheds of North Carolina, from north to south, are the Chowan-Roanoke, Albemarle Sound, Pamlico-Pungo River, Neuse River, Bay River, Newport River, White Oak River, New River, and Cape Fear River (Figure 1). These likewise feed into the major sounds of Albemarle-Currituck, Croatan, Roanoke, and Pamlico. Numerous smaller sounds exist south of Pamlico Sound but they are usually short in length or subject to more oceanic influences than freshwater runoff (Figure 1). Most of the major rivers of North Carolina have extensive watersheds and are usually 10m or less deep. The Cape Fear River, in the southern portion of the state, is the largest and is dredge-maintained upstream at 13 to 15m to Wilmington, North Carolina.

Albemarle and Currituck Sounds are typically freshwater habitats during most of the year. Spring freshet runoff of these freshwaters extend 28 km into the low saline 8 ppt to 20 ppt Croatan and Roanoke Sounds thereby carrying fresh waters southward to Oregon Inlet (Figure 1). During the late fall (November) saline waters from Croatan and Roanoke sounds may extend into and along the lower eastern third of Albemarle Sound.

The Pamlico-Pungo rivers are usually saline from near Washington and Winsteadville, North Carolina. Spring or sudden runoffs lower these 10 ppt to 17 ppt waters to 0 ppt for distances of 60 and 15 km respectively.

The short 5 km Bay River is not included in the discussions of this study as it usually does not have a clearly defined freshwater intrusion zone. Instead runoff waters flow out into Pamlico Sound as a layer over the highly saline bottom waters.

The Neuse River is fresh-water to just downstream of Grifton, North Carolina. The affected area of spring freshwater intrusion moves 0 ppt salinity waters 35 km to the junction of the Neuse River with Pamlico Sound. Surface waters of Pamlico Sound, during hurricane or other heavy rains, have been found fresh the entire extent from west to east and often pour out the inlets in the outer banks as a definite visible water mass (Schwartz 1973). However, 7 ppt to 32 ppt salinities usually prevail within Palmico Sound (Schwartz and Chestnut 1973).

The Newport River is a short compressed estuary of 12 km and is subject to large saline intrusions from the nearby Atlantic Ocean (Hyle 1976). The freshwater runoff zone has extended downstream for 4 to 5 km from its confluence with the estuary near the "Crossrocks."

The White Oak River is a long shallow river subject to high saline intrusions from the nearby ocean in its lower courses. During runoff the vertical freshwater face has been moved downstream 15 km to Stella, North Carolina.

The New River is another saline intrusion-influenced river, yet the runoff zone is often extended southeast of Jacksonville, North Carolina for 12 km.

The Cape Fear River is a swift river which, in its lower 30 km, is subject to 2-m tidal influences. Cape Fear experiences the highest

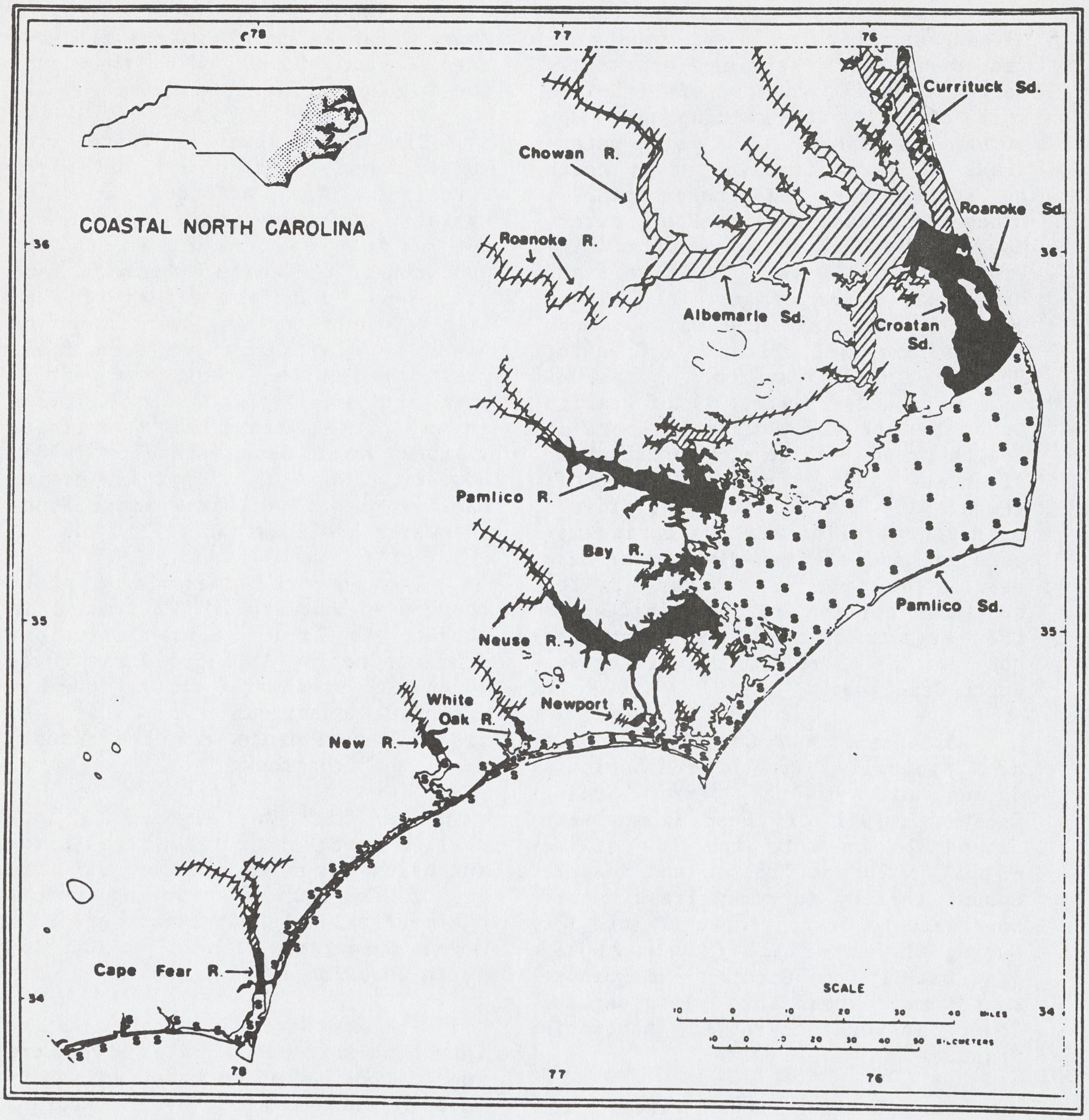

Figure 1. Major rivers and sounds of coastal North Carolina illustrating areas considered freshwater (/////), runoff or distrubed estuarine (▬) and saline (S) habitats.

runoff of any watershed, 257,929 to 7,264,664 liters/mo and flows of 66 cm/sec have been recorded (Schwartz et al. 1979a, b). However, that area from Campbell Island, 9 km south of Wilmington, North Carolina, to the man-made cut, "Snows Cut," 15 km further downstream is often subjected to periodic freshwater runoff which produces 0 ppt recordings throughout the 13-m deep waters for periods of 6 to 8 weeks (Schwartz et al. 1979a, b).

DISCUSSION

Hoagman and Wilson (1976), Lowe-McConnell (1975), and Schubel et al. (1976), have documented the natural or induced downstream shift of the oblique or vertical freshwater-saline interface of a coastal stream or river following a rain or hurricane. Others (Chesapeake Res. Cons. 1976) have noted the resiliency of these saline-depressed waters as they return to nearly "normal" states within short or long intervals but have not resolved the question--is this disturbed zone a truly freshwater or some sort of hybrid habitat? Likewise, what happens to the freshwater and marine fishes that are momentarily "trapped" within these temporary and rapidly chemically changing waters (Aller 1978; McHugh 1960)? It is to this unstable and temporary no man's land between fresh and saline waters that I now address this report.

RESULTS

To date only Schwartz (1964) has compiled a list of freshwater fishes that are known from runoff freshwater-euryhaline waters. Gunter (1942, 1956) compiled a similar list for 150 marine fishes known from euryhaline waters. Otherwise the sporadic occurrence of a species is usually treated as a brief note that one or more characteristically freshwater or marine fish was encountered in a freshwater, euryhaline, or marine habitat or vice versa (Rohde et al. 1979).

I now add to Schwartz's 28 (1964) and Gunter's 150 (1942, 1956) species lists of fishes that 37 freshwater (Table 1) and 77 marine (Table 2) fishes, within 13 freshwater and 38 marine families respectively, are known to frequent or live in "freshwater" runoff habitats within the major tributaries of North Carolina (Figure 1). Seven of the freshwater species were found in waters that were or reverted to 22 ppt to 31 ppt salinities following runoff. These included the longnose gar (Lepisosteus osseus), gizzard shad (Dorosoma cepedianum), golden shiner (Notemigonus chrysoleucus), white catfish (Ictalurus catus), brown bullhead (Ictalarus nebulosus), mosquitofish (Gambusia affinis, and flier (Centrarchus macropterus). Of these Schwartz (1964) had, elsewhere, collected the gar from 23.4 ppt, gizzard shad 22.6 ppt, golden shiner 14.4 ppt, and white catfish 14.5 ppt (Schwartz and Kendall 1968) waters. Twenty-five of the 37 freshwater fishes were found in higher salinities, in North Carolina, than previously noted by Schwartz (1964). In some cases, such as the gizzard shad, mosquitofish, bluegill, and pumpkinseed, their occurrences were recorded as abundant. Most of the freshwater fishes (20) were rare captures in the runoff zone, which reverted to 1 ppt to 27 ppt salinities. Thirteen species were common to zones that had been 1ppt to 31 ppt salinity Nine centrarchids and eight cyprinids were fishes that frequented the runoff disturbed areas for prolonged periods of 6 to 8 weeks prior to their retreat upstream into "pure" freshwater habitats. No trend was evident of increased number or kind of fish inhabiting the runoff area.

TABLE 1. List of 37 freshwater fishes, within 13 families, known to occur in previously considered estuarine waters of North Carolina when subjected to periodic flood water runoff.

Common-Scientific Name	Watershed								Max. Sal.	Prev. Lit.	New Sal. High	Status
	Cho	Alb	Pam	N	Np	WO	Ne	CF				
Gars - Lepisosteidae												
Longnose gar - Lepisosteus osseus	X	X	X	X	X	X	X	X	31	S	*	C
Bowfins - Amiidae												
Bowfin - Amia calva	X	X	X	-	-	-	-	X	5			R
Herrings - Clupeidae												
Gizzard shad - Dorosoma cepedianum	X	X	-	-	-	-	-	X	30	S	*	Abd
Mudminnows - Umbridae												
Eastern mudminnow - Umbra pygmaea	X	X	-	-	-	-	-	-	12	S	*	R
Pikes - Esocidae												
Chain pickerel - Esox niger	X	X	-	-	-	-	-	-	5	S	*	C
Minnows - Cyprinidae												
Carp - Cyprinus carpio	X	X	-	-	-	0	0	X	1	S		C
Silvery minnow - Hybognathus nuchalis	X	X	-	-	0	0	0	0	6	S	*	R
Golden shiner - Notemigonus crysoleucas	X	X	X	-	-	-	-	X	27	S		C
Ironcolor shiner - Notropis chalybaeus	-	-	-	-	-	0	-	-	6			R
Dusky shiner - Notropis cummingsae	0	0	-	-	0	-	-	X	2		*	R
Spottail shiner - Notropis hudsonius	X	X	-	-	0	0	0	-	4	S	*	R
Coastal shiner - Notropis petersoni	0	0	0	0	0	0	-	X	3		*	R
Swallowtail shiner - Notropis procne	X	-	0	0	0	0	0	0	1		*	R
Suckers - Catostomidae												
Creek chubsucker - Erimyzon oblongus	X	-	X	-	-	-	-	-	9	S	*	R
Shorthead redhorse - Moxostoma macrolepidotum	X	X	-	-	0	0	0	-	8	S	*	R
Freshwater catfish - Ictaluridae												
White catfish - Ictalurus catus	X	X	X	X	-	-	-	X	27	S	*	C
Blue catfish - Ictalurus furcatus	0	0	0	0	0	0	0	X	1		*	R
Yellow bullhead - Ictalurus natalis	X	X	-	-	-	-	-	-	5		*	R
Brown bullhead - Ictalurus nebulosus	-	-	X	-	-	-	-	X	27	S		R
Tadpole madtom - Noturus gyrinus	X	X	-	-	-	-	-	-	5		*	R
Margined madtom - Noturus insignis	X	0	-	-	-	X	-	-	5		*	R
Cavefishes - Amblyopsidae												
Swampfish - Chologaster cornuta	X	-	-	-	-	-	0	-	5		*	R
Pirate Perch - Aphredoderidae												
Pirate perch - Aphredoderus sayanus	X	X	X	-	X	-	-	X	5		*	R
Livebearers - Poeciliidae												
Mosquitofish - Gambusia affinis	X	X	X	X	X	-	-	X	22	S		Abd
Sunfishes - Centrarchidae												
Flier - Centrarchus macropterus	X	X	X	X	-	-	-	X	24		*	C
Banded pygmy sunfish - Elassoma zonatum	0	0	-	-	X	0	0	-	2		*	R
Bluespotted sunfish - Enneacanthus gloriosus	X	X	X	-	-	-	-	-	5	S		C
Redbreast sunfish - Lepomis auritus	X	X	-	-	-	-	-	-	7		*	C
Pumpkinseed - Lepomis gibbosus	X	X	X	X	-	X	-	-	15	S		Abd
Warmouth - Lepomis gulosus	X	X	X	-	-	-	-	-	7		*	R
Bluegill - Lepomis macrochirus	X	X	X	-	X	X	-	X	9	S		Abd
Largemouth bass - Micropterus salmoides	X	X	X	-	-	X	-	X	5	S		C
Black crappie - Pomoxis nigromaculatus	X	-	-	-	-	0	0	X	1.3		*	R
Perches - Percidae												
Swamp darter - Etheostoma fusiforme	X	-	X	-	-	-	0	X	5	S		C
Tessellated darter - Etheostoma olmstedi	X	X	-	-	0	-	-	X	6		*	C
Sawcheek darter - Etheostoma serriferum	-	-	-	X	-	-	-	-	8		*	C
Yellow perch - Perca flavescens	X	X	X	-	0	-	-	X	5	S		C

0 = not known from watershed
\- = known in watershed but not collected in disturbed portion
X = known from disturbed portion of watershed
Cho = Chowan River
Alb = Albemarle Sound, includes Currituck, Croatan and Roanoke Sounds
Pam = Pamlico River and Sound
N = Neuse River
Np = Newport River
WO = White Oak River
Ne = New River
CF = Cape Fear River
Max. Sal. = Maximum salinity in which specimen was captured
Prev. Lit. = Previous literature citation of either G (Gunter) or S (Schwartz)
* = established new high for recorded salinity observation
C = Common
R = Rare
Abd = abundant, yg = young
S = Schwartz 1964
G = Gunter 1942, 1956

TABLE 2. List of 77 marine fishes, within 38 families, known to occur in previously considered estuarine waters of North Carolina which tolerate 0 ppt salinities for prolonged periods when the estuary is subjected to periodic flood water runoff. (See Table 1 for explanation of symbols.)

Common-Scientific Name	Watershed								Prev. Lit.	Status
	Cho	Alb	Pam	N	Np	WO	Ne	CF		
Lampreys - Petromyzontidae										
Sea lamprey - Petromyzon marinus	-	X	-	X	-	-	-	X	G	R
Requiem Sharks - Carcharhinidae										
Atlantic sharpnose shark - Rhizoprionodon terraenovae	0	0	-	-	X	X	X	X	G	C
Skates - Rajidae										
Clearnose skate - Raja eglanteria	0	0	0	-	X	X	X	X		C
Stingrays - Dasyatidae										
Southern stingray - Dasyatis americana	0	0	X	X	X	X	X	X		R
Atlantic stingray - Dasyatis sabina	0	0	0	0	X	X	X	X	G	C
Sturgeons - Acipenseridae										
Atlantic sturgeon - Acipenser oxyrhynchus	X	X	X	X	X	X	X	X	G	Abd
Freshwater Eels - Anguillidae										
American eel - Anguilla rostrata	X	X	X	X	X	X	X	X	G	Abd
Conger Eels - Congridae										
Conger eel - Conger oceanicus	0	0	-	-	X	X	X	X		C
Snake Eels - Ophichthidae										
Shrimp eel - Ophichthus gomesi	0	0	-	-	X	X	X	X		C
Herrings - Clupeidae										
Atlantic menhaden - Brevoortia tyrannus	X	X	X	X	X	X	X	X	G	Abd
Blueback herring - Alosa aestivalis	X	X	X	X	X	X	X	X	G	Abd
Hickory shad - Alosa mediocris	X	X	X	X	X	X	X	X	G	Abd
Alewife - Alosa pseudoharengus	X	X	X	X	X	X	X	X	G	Abd
American shad - Alosa sapidissima	X	X	X	X	X	X	X	X	G	Abd
Threadfin shad - Dorosoma petenense	0	0	X	X	-	-	-	X		Abd
Atlantic thread herring - Opisthonema oglinum	-	-	X	X	X	-	-	X		C
Anchovies - Engraulidae										
Striped anchovy - Anchoa hepsetus	-	X	X	X	X	-	-	X		C
Bay anchovy - Anchoa mitchilli	X	X	X	X	X	X	X	X	G	Abd
Toadfishes - Batrachoididae										
Oyster toadfish - Opsanus tau	0	0	X	X	X	X	X	X		C
Clingfishes - Gobiesocidae										
Skilletfish - Gobiesox strumosus	0	0	-	-	X	X	X	X		C
Codfishes - Gadidae										
Spotted hake - Urophycis regius	0	0	X	X	X	X	X	X		C
Cusk-eels - Ophidiidae										
Crested cusk-eel - Ophidion welshi	0	0	0	0	-	-	-	X		R
Needlefishes - Belonidae										
Atlantic needlefish - Strongylura marina	X	X	X	X	X	X	X	X	G	C
Killifishes - Cyprinodontidae										
Sheepshead minnow - Cyprinodon variegatus	0	0	X	X	X	X	-	X	G	C
Banded killifish - Fundulus diaphanus	X	X	X	-	X	0	X	-		C
Mummichog - Fundulus heteroclitus	0	0	X	-	X	X	X	X	G	C
Striped killifish - Fundulus majalis	0	0	-	-	-	-	-	X		C
Rainwater killifish - Lucania parva	0	0	X	X	0	0	0	0	G	R
Silversides - Atherinidae										
Rough silverside - Membras martinica	0	0	X	X	-	0	0	X	G	C
Tidewater silverside - Menidia beryllina	X	X	X	X	X	X	X	X	G	Abd
Atlantic silverside - Menidia menidia	0	X	-	X	X	X	X	X	G	Abd
Pipefishes - Syngnathidae										
Lined seahorse - Hippocampus erectus	0	0	X	X	X	X	X	X		C
Northern pipefish - Syngnathus fuscus	0	0	-	-	-	-	-	X		C
Chain pipefish - Syngnathus louisianae	0	0	-	-	-	-	-	X		C
Snooks - Centropomidae										
Snook - Centropomus undecimalis	0	0	-	0	0	0	0	X		R
Temperate Basses - Percichthyidae										
White perch - Morone americana	X	X	X	X	-	-	-	X	G	Abd
Striped bass - Morone saxatilis	X	X	X	X	X	X	X	X	G	Abd
Sea Basses - Serranidae										
Black sea bass - Centropristis striata	0	0	-	-	X	X	X	X		R (yg)
Bluefishes - Pomatomidae										
Bluefish - Pomatomus saltatrix	0	-	X	X	X	X	X	X		Abd (yg)
Jacks - Carangidae										
Crevalle jack - Caranx hippos	0	0	-	-	X	X	X	X	G	C
Atlantic bumper - Chloroscombrus chrysurus	0	0	-	-	X	X	X	X		R
Snappers - Lutjanidae										
Gray snapper - Lutjanus griseus	0	X	X	X	X	X	X	X	G	R
Mojarras - Gerreidae										
Spotfin mojarra - Eucinostomus argenteus	0	0	-	-	X	X	X	X		R
Grunts - Pomadasyidae										
Pigfish - Orthopristis chrysoptera	0	0	X	X	X	X	X	X		C
Porgies - Sparidae										
Sheepshead - Archosargus probatocephalus	0	0	-	-	X	-	X	X	G	C (yg)
Pinfish - Lagodon rhomboides	0	0	X	X	X	X	X	X	G	Abd
Drums - Sciaenidae										
Silver perch - Bairdiella chrysura	0	0	X	X	X	X	X	X		C
Spotted seatrout - Cynoscion nebulosus	0	0	X	X	X	X	X	X		C
Weakfish - Cynoscion regalis	0	0	X	X	X	X	X	X	G	C
Spot - Leiostomus xanthurus	0	0	X	X	X	X	X	X	G	C
Southern kingfish - Menticirrhus americanus	0	0	-	-	X	X	X	X		C
Atlantic croaker - Micropogonias undulatus	0	0	X	X	X	X	X	X	G	C
Black drum - Pogonias cromis	0	0	X	X	X	X	X	X	G	Abd (yg)
Red drum - Sciaenops ocellata	0	0	X	X	X	X	X	X	G	C
Star drum - Stellifer lanceolatus	0	X	X	X	X	-	-	X		C
Mullets - Mugilidae										
Striped mullet - Mugil cephalus	X	X	X	X	X	X	X	X	G	Abd
White mullet - Mugil curema	0	0	X	X	X	X	X	X	G	Abd
Stargazers - Uranoscopidae										
Southern stargazer - Astroscopus y-graecum	0	0	-	-	X	X	X	X		R
Combtooth blennies - Blenniidae										
Crested blenny - Hypleurochilus geminatus	0	0	-	X	X	X	X	X		C
Freckled blenny - Hypsoblennius ionthas	0	0	0	0	0	0	0	X		R
Sleepers - Eleotridae										
Fat sleeper - Dormitator maculatus	0	0	0	0	0	-	0	X	G	R
Gobies - Gobiidae										
Lyre goby - Evorthodus lyricus	0	0	0	0	0	0	0	X	G	R
Darter goby - Gobionellus boleosoma	0	0	0	0	X	-	-	X	G	R
Sharptail goby - Gobionellus hastatus	0	0	-	-	X	X	X	X		C
Freshwater goby - Gobionellus shufeldti	0	0	-	-	X	-	-	X	G	R
Naked goby - Gobiosoma bosci	0	0	-	-	X	X	X	X	G	C
Butterfishes - Stromateidae										
Harvestfish - Peprilus alepidotus	0	0	X	X	X	X	X	X		C
Searobins - Triglidae										
Bighead searobin - Prionotus tribulus	0	X	X	X	X	X	X	X		C
Lefteye flounders - Bothidae										
Ocellated flounder - Ancylopsetta quadrocellata	0	0	-	X	X	X	X	X		C
Bay whiff - Citharichthys spilopterus	0	0	-	X	X	X	X	X	G	C
Fringed flounder - Etropus crossotus	0	0	-	-	-	-	-	X		C
Summer flounder - Paralichthys dentatus	X	0	X	X	X	X	X	X	G	Abd
Southern flounder - Paralichthys lethostigma	0	0	X	X	X	X	X	X	G	C
Broad flounder - Paralichthys squamilentus	0	0	X	X	X	X	X	X		R
Windowpane - Scophthalmus aquosus	0	0	X	X	X	X	X	X		Abd
Soles - Soleidae										
Hogchoker - Trinectes maculatus	X	X	X	X	X	X	X	X	G	Abd
Tonguefishes - Cynoglossidae										
Blackcheek tonguefish - Symphurus plagiusa	0	0	-	X	X	X	X	X		Abd (yg)

Of the marine fishes found in freshwater runoff areas, all 77 listed (Table 2) were found in 0 ppt salinity waters for extended periods as long as six weeks. As expected, anadromous, catadromous, and diadromous fishes such as sturgeon, herrings, shad, and eels also were abundant in the 0 ppt runoff water zones. Other abundant fishes within the runoff area were the bay anchovy; tidewater and Atlantic silversides; white perch; striped bass; bluefish (young); sheepshead (yg); pinfish (yg); black drum (yg); striped and white mullet; summer, southern, and windowpane flounders; hogchokers; and blackcheek tonguefish (Table 2). Thirty-seven of the 77 marine or euryhaline fishes were common to the various disturbed runoff watersheds of the state while only 15 were rare occurrences within these waters. Herrings (9 species), drums (7), and flounders (7) were the dominant groups of fishes captured in the runoff zones. Thirty-five of the 77 marine fishes occurred in 0 ppt waters and had not been reported previously by Gunter (1942, 1956).

Of the fishes encountered within the runoff zone, most were small juvenile or one-year-old age class individuals. Some species, such as the drums and flounders, were known to migrate to low salinity nursery waters and hence their presence in the runoff zone could be accounted for by such behaviors (Marshall 1976; Weinstein 1979, 1980). None exhibited external signs of stress or emaciation as a result of their living in or encounter with the runoff zone.

The presence or absence of several species within a watershed or the runoff area was also a function of zoogeography (Jenkins et al. 1972; Rohde et al. 1979) rather than runoff or environment, as North Carolina lies at the junctures of many coastal north and south ranging species. Like Gunter et al. (1974) presence or absence of a freshwater or marine fish in a runoff area was dependent on many other factors, expecially water temperature and oxygen content.

Water temperatures and oxygen levels, in most areas, of North Carolina were not limiting factors as most runoff occurred during months when water temperatures were low and contained high levels of oxygen (see Schwartz 1973; Schwartz et al. 1979a, b, six-year study of Cape Fear River). Whether the varying chemical content of the various watersheds (Geraghty et al. 1973) played a role in the enhancement or demise of a species that was subjected to the sudden runoff waters remains unknown.

Likewise nutrient change, as a result of runoff, is poorly known for North Carolina waters, the exception being the Neuse River where Hobbie and Smith (1975) noted the effects of runoff on various environmental parameters.

Nichols (1977), Schubel and Hirschberg (1978), and many others have documented the enormous sediment changes that can occur in a body of water which has been subjected to river floods. Giese et al. (1979), reviewing the hydrology of the major estuaries of North Carolina, noted the effects of sediment "salting out" following freshwater inflow and calculated the number of days one could expect upriver portions of major rivers to be drastically affected by this phenomenon. Edgwald (1972) and Griffin and Ingram (1955) reviewed the sediments of coastal Pamlico and Neuse Rivers as a result of runoff. In turn, these sediments most likely caused changes in bottom chemical conditions (Aller 1978) or bottom macroinvertebrates faunas (Schwartz et al. 1979a, b) on which the runoff zone fishes fed (Schwartz et al. 1980). Yet little information exists, in North Carolina, on the fate of freshwater fishes, their transport into or within the runoff area, and how they are affected by sediments (Custer and Ingram 1974).

CONCLUSIONS AND RECOMMENDATIONS

Many aspects remain unresolved in relation to fishes and the runoff zone and will provide research for the future. Thus, we must take the next step and test various species, under a variety of sudden or runoff conditions (Livingston et al. 1976), to determine why some cyprinids, centrarchids, clupeids, sciaenids, and bothids can exist in the unstable environment caused by freshwater runoff while others cannot. Only then will we begin to understand a runoff habitat, a fish's needs, and how we can best assure its survival in these rapidly changing runoff waters and habitats.

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LITERATURE CITED

Abbott, D.; Dawson, C.E.; Oppenheimer; C.H. Physical, chemical, and biological characteristics of estuaries. Water and pollution handbook. New York: Marcel Dekker Inc., N.Y. Vol. 1.; 1971. 51-140.

Aller, R.C. The effects of animal-sediment interactions on geochemical processes near the sediment-water interface. Wiley, M. L. ed. Estuarine interactions. New York, NY: Academic Press; 1978: 157-172.

Carr, A.; Goin, C. J. Reptiles, amphibians and freshwater fishes of Florida. Gainesville: Univ. Fla. Press; 1955: 341p.

Caspers, H. Estuaries: Analysis of definitions and biological considerations. Lauff, G. H. ed. Estuaries. Washington, DC: Amer. Assoc. Adv. Sci., Pub. 83; 1967.

Chesapeake Research Consortium. The effects of tropical storm Agnes on the Chesapeake Bay Estuarine System. Ches. Res. Consort. Publ. 54, Baltimore, MD: Johns Hopkins Univ. Press; 1976.

Custer, E.S., Jr.; Ingram; R.L. Influence of sedimentary processes on grain size distribution curves of bottom sediments in the sounds and estuaries of North Carolina. Univ. No. Carolina Sea Grant Publ. UNC-SG-74-13; 1974. 88p.

Dahl, E. Ecological sedentary boundaries of Poikilohaline water. Oikos 7:1-23; 1956.

Douglas, N.H. Freshwater fishes of Louisiana. Baton Rouge, LA: Claitor's Publ. Div.; 1974.

Edgwald, J.K. Coagulation in estuaries. Univ. No. Carolina Sea Grant Publ. UNC-SG-72-06; 1972: 204p.

Geraghty, J.J.; Miller, D.W.; von der Leeden, F.; Troise, F.L. Water atlas of the United States. Washington, New York: Water Info. Center Publ. Port 1973; 119 p.

Giese, G.L.; Wilder, H.B.; Parker, G.C., Jr. Hydrology of major estuaries and sounds in North Carolina. U.S. Geol. Surv. Water Res. Investig. 79-46, 1979; 175p.

Griffin, G.M.; Ingram, R.L. Clay minerals of the Neuse River Estuary. Sediment. Petrol. 25(3): 194-200; 1955.

Gunter, G. A list of the fishes of the mainland of North and Middle America recorded from both freshwater and sea water. Amer. Midl. Nat. 28(2):305-326; 1942.

Gunter, G. A revised list of euryhaline fishes of North and Middle America. Amer. Midl. Nat. 56 (2):345-354; 1956.

Gunter, G.; Ballard, B. S.; Venkataraniah, A. A review of salinity problems of organisms in Central States Coastal area subject to the effects of engineering works. Gulf Res. Rep.4(3): 380-475; 1974.

Hedgpeth, J.W. The classification of estuarine and brackish waters and the hydrographic limits. Rep. 11 Nat. Res. Comm. 1951: 49-56.

Hedgpeth, J. W. Estuaries and lagoons II. Biological aspects. Hedgpeth, J. W. ed. Treatise on marine ecology and paleocology. Vol. 1, Hedgpeth, J. W. ed. Mem. 67 Geol. Soc. Amer. Vol. 1; 1957: 643-729.

Hoagman, W.J.; Wilson, W.L. The effects of tropical storm Agnes on fishes in the James, York, and Rappahannock Rivers of Virginia, The effects of tropical storm Agnes on the Chesapeake Bay Estuarine System. Chesapeake Res. Consort. Inc. Publ. 54; 1976: 464-477.

Hobbie, J.E.; Smith, N.W. Nutrients in the Neuse River Estuary. Univ. No. Carolina Sea Grant Publ. UNC-SG-75-21; 1975: 183p.

Hoar, W.S.; Randall, D.J. eds. Fish physiology. VIII. Bioenergetics and growth. New York: Academic Press, 1979. 786p.

Hyle, A.K., II. Fishes of the Newport River Estuary, North Carolina, their composition, seasonality, and community structure. Chapel Hill, N.C.: Univ. No. Carolina; 1976: 192p.

Jenkins, R. E.; Lachner, E. A.; Schwartz, F.J. Fishes of the central Appalachian drainages: Their distribution and dispersal, Holt, P. C. ed. The distributional history of the Southern Appalachians Pt. III Vertebrates. Blacksburg, Va.; 1972: 43-117.

Kinne, O. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. Oceanogr. Mar. Biol. Annu. Rev. 2: 281-399; 1964.

Kinne, O. Physiology of estuarine organisms with special reference on salinity and temperatures. General aspects. Amer. Assoc. Adv. Sci. Publ. 83:525-540; 1967.

Lauff, G.H. editor. Estuaries. Amer. Assoc. Adv. Sci. Publ. 83, 1967. 757p.

Livingston, R. J.; Cripe, C. R.; Laughlin, R.A.; Lewis, F.G., III. Avoidance responses of estuarine organisms to storm water runoff and pulp mill effluents, Estuarine processes, Vol. 1. New York: Academic Press, Inc., 1976: 313-331.

Livingston, R. J.; Kobylinski, G. J.; Lewis, F.G., III; Sheridan, P.F. Long-term fluctuation of epibenthic fish and invertebrate populations in Apalachicola Bay, Florida. Fish. Bull. 74(2):311-322; 1976.

Livingston, R. J.; Sheridan, P. S.; McLane, B. G.; Lewis, F. G.,III; Kobylinski, G. J. The biota of the Apalachicola Bay system: Functional relationship, Proceedings of a conference on the Apalachicola drainage system. Fla. Mar. Res. Publ. 26; 1977: 75-100.

Lowe-McConnell, R.H. Fish communities in tropical freshwater. New York: Longman. 1975: 337p.

Marshall, H.L. Effects of mosquito control ditching on Juncus marshes and utilization of mosquito control ditches by estuarine fishes and invertebrates. Chapel Hill, N.C.: Univ. No. Carolina, 1976. 294p. Dissertation.

McHugh, J.L. The pound-net fishing in Va. Pt. 2. Species composition of landings reported as menhaden. Comm. Fish. Rev. 22 (2):1-16; 1960.

McHugh, J. L. Management of estuarine fisheries, Smith, R. F.; Swartz, A. H.; Massman, W. H. eds. A symposium on estuarine fisheries. Washington, D.C: Amer. Fish. Soc. Spec. Publ. 3. 1966: 133-154.

McHugh, J. L. Estuarine nekton. Lauff, G. A. ed. Estuaries. Washington, DC: Amer. Assoc. Adv. Sci. Publ. 83; 1967.

Myers, G. S. Freshwater fishes and West Indian Zoogeography. Annu. Rept. Smiths. Inst. Publ. 3451: 339-364 for 1937; 1938.

Myers, G. S. Use of anadromous, catadromous and allied terms for designating fishes. Copeia 1949 (2):89-96; 1949a.

Myers, G. S. Salt-tolerance of freshwater fish groups in relation to zoogeographical problems. Bidjr. Dierkande (Leiden) 27:315-322; 1949b.

Myers, G. S. Freshwater fishes and East Indian Zoogeography. Stanford Icthyol. Bull. 4(1):11-21; 1951.

Nichols, M.M. Response and recovery of an estuary following a river flood. J. Sediment. Petrol. 47 (3):1171-1186; 1977.

Odum, H.T. Factors controlling marine invasion into Florida freshwaters. Bull. Mar. Sci. Gulf. Caribb. 3:134-156; 1953.

Pritchard, N.W. What is an estuary: physical viewpoint. Lauff, G.H., ed. Estuaries. Washington DC: Amer. Assoc. Adv. Sci. Publ. 83; 1967a.

Pritchard, N. W. Observations of circulation in Coastal Plain estuaries. Lauff, G.H. ed. Estuaries. Washington, DC: Amer. Assoc. Adv. Sci. Publ. 83; 1967b; 37-44.

Rohde, F.C.; Burgess, G.H.; Link, G.W. Jr. Freshwater fishes of Croatan National Forest, North Carolina, with comments on the zoogeography of coastal plain fishes. Brimleyana 2: 97-118; 1979.

Schubel, J.R.; Carter, H.H.; Cronin, W.B. Effects of Agnes on the distribution of salinity along the main axis of the bay and in contiguous shelf waters. Effects of tropical storm Agnes on the Chesapeake Bay estuarine system. Chesapeake Res. Consort. Publ. 54; 1976: 33-65.

Schubel, J.R.; Hirschberg, D.J. Estuarine graveyards,climate change, and the importance of the estuarine environment. Wiley, M. L. ed. Estuarine interactions. New York: Academic Press; 1978: 285-303.

Schwartz, F.J. Natural salinity tolerances of some freshwater fishes. Underwat. Nat. 2(2): 13-15; 1964.

Schwartz, F. J. Biological and environmental assessment of four navigation improvement areas to Croatan, Roanoke, and Pamlico Sounds, North Carolina. Wilmington, DL: Rept. U.S. Corps Engineers. DACW 54-72-C-0047; 1973: 75p.

Schwartz, F.J.; Chestnut, A.F. Hydrographic atlas of North Carolina estuarine and sound waters, 1972. UNC-SG-73-12 Sea Grant Publ.; 1973: 132p.

Schwartz, F. J. Kendall, A. Lethal temperatures and salinity tolerances for white catfish, for white catfish, Ictalurus catus, from the Patuxent River, Maryland. Chesapeake Sci. 9(2): 103-108; 1968.

Schwartz, F.J.; Morgan, S.; McAdams, M.; Sandoy, K.; Mason, D. Food analyses of selected fishes captured in Cape Fear estuary and adjacent Atlantic Ocean, North Carolina, 1973-1978. Carolina Power Light Co. Pts. 1, 2, 3, Morehead City, NC: Inst. Mar. Sci. 1980; 1100p.

Schwartz, F. J.; Perschbacher, P.; McAdams, M.; Davidson, L.; Sandoy, K.; Simpson, C.; Duncan, J.; Mason, D. A summary report 1973-1977. An ecological study of fishes and invertebrate macrofauna utilizing the Cape Fear River estuary, Carolina Beach Inlet, and adjacent Atlantic Ocean. Carolina Power Light Co. Morehead City, NC: Inst. Mar. Sci. XIV: 1979a: 571p.

Schwartz, F. J.; Perschbacher, P.; McAdams, M.; Simpson, C.; Sandoy, K.; Duncan, J.; Tate, J.; Mason, D. An ecological study of fishes and invertebrate macrofauna utilizing the Cape Fear River estuary, Carolina Beach Inlet, and adjacent Atlantic Ocean. Annu. Rept. for 1978. Carolina Power Light Co. Morehead City, N.C.: Inst. Mar. Sci. XV; 1979b: 326p.

Symposium on the Classification of Brackish Waters. Venis 8-14 April. Centro Naz. Studi Talassograf. Consiglio. Naz. Richerche XI; Suppl.; 1958: 5-248.

Valikanges, I. Uber die biologie der Ostee als Brakwassergebiet. Verh. Int. Ver. Theor. Angew. Limnolog. 6; 1933.

Weinstein, M. P. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River North Carolina. Fish. Bull. 77(2):339-357; 1979.

Weinstein, M. P.; Weiss, S. L.; Hodson, R. G.; Gerry, L. R. Retention of three taxa of post larvae fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. Fish. Bull. 78(2): 419-436; 1980.

Wiley, M. L. ed. Estuarine Interactions. New York: Academic Press, 1978. 603p.

Williams, A.B.; Deubler, E.E., Jr. A ten-year study of meroplankton in North Carolina Estuaries. Assessment of Environmental Factors and sampling success among Bothid flounders and Penaeid shrimps. Chesapeake Sci. 9(1):27-41; 1968.

Williams, A. B.; Posner, G.S.; Woods, W. J.; Deubler, E. E., Jr. A hydrographic atlas of larger North Carolina Sounds. Univ. No. Carolina Sea Grant Publ. UNC-SG-73-02, 1973; 129p.

Reprint from:

Proceedings of the National Symposium on Freshwater Inflow to Estuaries. Vol. 1. p. 282-294. R. D. Cross and D. L. Williams (eds.). U. S. Fish Wildl. Serv. Biol. Serv. Progr. FWS/OBS-81/04, October 1981.

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DEPTH AND STORAGE CAPACITY CHANGES IN CHEAT LAKE, WEST VIRGINIA, DURING THE 64-YEAR PERIOD 1926–1990

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Abstract: Cheat Lake, a 20.8 km impoundment on Cheat River just south of the Pennsylvania/West Virginia state line, was constructed in 1926 to stem the floods that were common to the river. Changes in the holding capacity and bottom profiles as a result of siltation and scouring are reviewed following lake surveys in 1956 and 1990. A severe 1985 flood apparently reversed the siltation noted in 1956 through scouring of the upper and lower reaches of the lake. Today, plans to lumber the upper Cheat Basin will induce a return of siltation and filling in of the lake.

Key Words: Cheat Lake; storage capacity changes; West Virginia; siltation; flood effects.

INTRODUCTION

Cheat River, draining 3,688.2 sq. km (1,424 sq. mi.) of land in West Virginia, is the second largest tributary to the Monongahela River, which in turn is a tributary of the Ohio River. Forty-three floods have been recorded for the river between 1912 and 1940 (Cong. Rec., 1942). Only two major floods have occurred within the early history of the Cheat River Basin; they were in 1907 and 1936 (U.S. Dept. Comm. Weather Bur., 1955; Grover and Lichtblau, 1937). The most recent major flood occurred 3–5 November 1985 (West Penn Power Co., McCullough, pers. comm.).

A dam was constructed in 1926 about 5.6 km upstream of Cheat River's confluence with the Monongahela River and Point Marion, Pennsylvania, in order to curb the vast fluctuating flows and floods of the river with maximum and minimum predam flows at Ices Ferry which were 4,674.2 cu m/sec (156,000 cu ft./sec) on 10 July 1888 and 2.7 cu m/sec (95 cu ft./sec) on 7 October 1904, respectively. Originally the lake behind the dam was called Lake Lynn but since has commonly been referred to as Cheat Lake.

Little attention, other than Carpenter and Herndon's chemical analyses (1928, 1930), was given the lake's waters and fauna until the 1950s (Burley, 1955; Core, 1959; Schwartz, 1956). Schwartz and students began an intensive water quality, chemical, silt, and productivity study of Cheat Lake in 1955–1956 and expanded it to encompass the entire Cheat watershed (Schwartz, 1956). At that time silt influx had reduced the lake to 75.6% of its original capacity and several predictions were made as to the future extent of the silting in and fate of the lake.

Few have repeated their original studies to ascertain what has happened in the interim or to check how accurate their predictions may have been. A resurvey of

FIG. 1. Map of Cheat Lake and surrounding area in West Virginia mentioned in the text (Morgantown Quadrangle). Circled numbers are silt deposition transect stations used to obtain siltation

Cheat Lake's depths and holding capacity made 34 years later, 12–13 July 1990, addressed the following questions: what is the present holding capacity of the lake as compared to that determined in 1956; has siltation and filling in increased; is there a visible island, as predicted, near Mount Chateau; have the lake's bottom and mean depth profiles changed from that noted in 1956; and what may have caused these changes?

CHEAT LAKE

Cheat Lake lies north to south in Monongalia County, West Virginia, just south of the Pennsylvania–West Virginia state line. The first known white settler arrived in the Cheat Valley in 1754 (Callahan, 1923), but Moreland (1940) states that the first white settlers didn't arrive until 1772 and settled near what is now Cheat Lake. With settlement, 6–8 iron works and coal mines were active by 1840 at Sunset Beach and Canyon, West Virginia, and the Cheat River Basin had been logged over between 1840 and 1913 (Callahan, 1923).

The original site for Cheat Lake was a series of bottomlands nestled between mountains and ridges, covered by timber and heavy vegetation, that varied in height from 335 m to 518 m at Coopers Rock upstream of Mt. Chateau (Figs. 1 and 2). The original brush and trees were not removed prior to flooding. With time most of the original trees have decayed and few submerged areas of the original forest still persist in the lake today.

Cheat Lake was constructed in 1926 by West Penn Power Company. The dam created a lake 20.9 km long and 0.8 to 1.2 km wide (Fig. 1). Its original surface acreage was 700.4 ha (1,730 ac.) and the mean depth 12.8 m. The headwater elevation of the lake was 264.5 m, the tailwater elevation 238 m, and maximum pool elevation of the lake was 264.5 m. The normal power head was 24.8 m. The power plant usually operated during weekday mornings and afternoon peak periods; the lake refilled during off-peak periods. When the river flow was greater than "normal," the plant operated to obtain maximum energy from the available water. The lake in recent years is drawn down 2+ m in November in anticipation of spring runoff flow waters.

Originally one road, W. Va. 73, crossed Cheat Lake at Ices Ferry, a smaller road crossed Rubbles Run near the dam. A second road and a newer bridge were constructed in 1972 across the lake a few hundred meters north of the Ices Ferry bridge to accommodate U.S. 48.

The waters of Cheat Lake in 1956 were rust colored from the nearby and upriver acid mine runoff tributary waters, existent in the late 1880s and early 1900s, located especially on the western side of the lake from Grammy's Run (R, near the U.S. 48 Sunset Beach bridge) at Canyon, and all western tributaries northward to Sugar Grove, near the dam (Fig. 1). In 1956 most eastern tributaries to Cheat Lake were natural flowing streams (Schwartz, 1956). Coal from the mines fed the iron works at Laurel, Canyon, and Stewart Towers.

←
rates in 1956. Streams A–G were acid mine (west shore) and H–R natural flowing in 1956. * is site of new U.S. 48 Bridge. Dam is located just at the Pa/W. Va. state line.

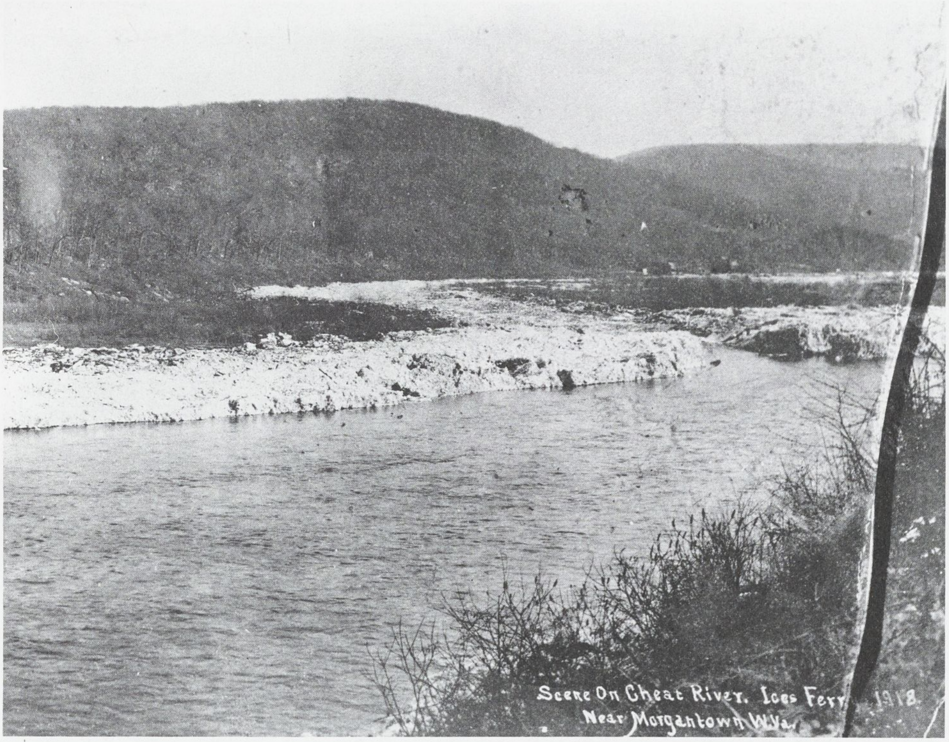

FIG. 2. View of Cheat River south of Ices Ferry in 1918 illustrating steep vegetated terrain prior to Cheat Lake construction. Note, on left side, the area predicted to become exposed and referred to, in the text, as the ball field, has continued to shoal up and is often exposed during present day draw downs of the lake. Photo from West Virginia and Regional History Collection, West Virginia University Library, Morgantown, W. Va.

Today, effluents from most of the acid mine streams have been sealed, and the coal conveyer across the lake at Canyon has been removed. Nevertheless, the ferrous iron flocculants that formed, following acid mine water discharge into the lake, and remained in suspension for several years are still present. Today (1990) the iron flocculants have still not gone into solution and can be resuspended by disturbing the grey-green colored lake's substrate where they have settled out. Man's presence is more evident today because of the numerous marinas at Mt. Chateau, Sunset Beach, and Canyon. The lake has become a highly used recreation site by the populace that has settled around the lake or travels there from afar; whereas in 1956 the only evidence of man was the seasonal sparse use of the Mt. Chateau lodge just south of Ices Ferry.

METHODS

1956: Sixty-four transects (A) were made across the lake from Grassy Island to the dam. Depths were determined every 30.5 m along each transect with a lead line. Markers located on each shore helped align a skiff and keep it on station while transversing a transect. Original bottom depths and mean depths, deter-

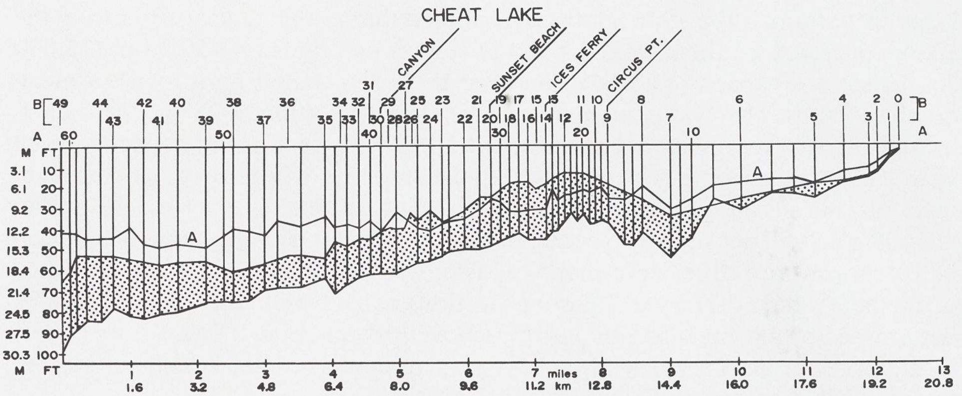

FIG. 3. Cross section configuration of Cheat Lake illustrating original lake depths, mean survey depths along 64 transects in 1956 (A) and 49 transects in 1990 (B) from just south of Grassy Island northward to the dam. Stippled areas are mud deposits presently below mean water depths recorded in July 1990. Note filling in between Circus Point and Ices Ferry (transects 9–14) with scouring evident in the upper lake (transects 5–8) and lower lake (transects 26–dam) in 1990.

mined in 1956, were plotted as a side profile of the lake (Fig. 3) to depict what depth changes had occurred since the lake's construction.

1990: Forty-nine transects (B) were made across Cheat Lake, six in Rubbles Run, and two in Sunset Beach harbor, at or near the original 1956 transects (Fig. 3). A continuous stylus chart recording Lowrance X-15 depth recorder was used to note the bottom profiles along each transect. Since a single crossing of each transect took only a few minutes, no shore markers were used as in 1956. A 5.1 m Sun Ray skiff propelled with a Mercury 3L inboard–outboard motor was operated at 1,000 RPMs or 1.7 m sec. A transducer was mounted on the transom 0.49 m below the water surface; all depth recordings were corrected for this positioning. Vessel speed and distances were calibrated against the known lengths of Ices Ferry bridge (203.3 m) and the new U.S. 48 bridge which is 523 m long (data furnished by W. Va. Dept. Highways). To obtain mean depths along a transect, depths were calculated every 9.1 m along the transect. These data were averaged to obtain the mean transect depth plotted in Figure 3. A further depth adjustment was made in that on 12 July 1990 the lake pool was 0.7 m below maximum pool of 264.5 m (West Penn Power data, McCullough, pers. comm.). Bottom profiles were also compared to those noted for Ices Ferry taken in 1921 and the new U.S. 48 bridge in 1929 and 1972 (W. Va. Dept. Highways construction map data).

OBSERVATIONS

1956 findings and predictions: Cheat Lake in 1956 was determined to be oligotrophic as a result of the acid mine and paper pulp pollutions entering the lake; the former from coal mines and iron works located along the western shores of the lake and the latter from lumber and pulp mill operations upriver of the lake near Parsons, West Virginia. These pollutants severely affected and influenced the meager fish and invertebrate faunas inhabiting the lake (Schwartz, 1956).

More importantly, the 1956 survey determined that in the 28 years following the lake's construction, the lake had silted in so that its original 8,960 ha-m (73,000 ac.-ft.) storage capacity had been reduced to 75.6% (6,860 ha-m) with a mean depth of 9.8 m. This was equivalent to 3.0 m silt deposition in 28 yr. These data, in other terms, represented a sheet of silt 106.7 mm deep being deposited each year, if evenly distributed throughout the lake. In terms of hectares of land brought in as silt, the silt accumulation amounted to 20.4 ha (50.5 ac.) per month or 245 ha (605.5 ac.) fill per year. Projecting that data further, an average rate of siltation of 106.6 mm or a little more than 0.325 in. was deposited each of the 28 years of the lake's then existence. Those projections agreed well with the 112 mm/yr determined by placing 0.55 liter jars (in sets of three suspended on anchored lines) located at 5 m depths every 30 m along six transects (circled numbers) located between Mt. Chateau and the dam (Fig. 1).

The jar collection method also confirmed that silt deposition was not uniform throughout the lake, being greatest between Circus Point and the Canyon coal conveyer area. Those observations were the basis on which it was predicted that a large visible island, then only 3.7 m below the surface, would develop on the east shore of the lake near Mt. Chateau. Other predictions were that the Sunset Beach tributary area would be completely filled in with silt and mud so that only a small stream would flow down over the ensuing mud flat in 90 years. Likewise, it was estimated that as a whole the lake would be completely filled in 92 years even though it was thought then that siltation rates would increase through the years as the upper Cheat River Basin was logged over.

1990 observations: Contrary to expectations that Cheat Lake would continue to fill in following the 1956 survey, Cheat Lake in 1990 has an average depth of 11.9 m (Fig. 3) or a storage capacity of 8,330 ha-m (67,470 ac.-ft.), 92.4% of its original storage capacity and represents a loss of an average of 2.2 m of fill or 76.6 ha/month or 919.2 ha/yr in the 34 yr span 1956–1990. The most surprising features are that the areas upriver of Circus Point and below Canyon have been drastically scoured (Fig. 3), apparently during the 3–5 November 1985 flood waters that passed through the lake at volumes of 3,266–4,787.5 cu-m/sec (West Penn Power data, McCullough, pers. comm.). As predicted in 1956 the area between Mt. Chateau and the Ices Ferry bridge has continued to shoal such that the island predicted then is only 1.4 m at pool below the surface. With the present day practice of lowering the lake level in November this area is often exposed and is locally referred to as the "ball field" (see Fig. 2). Note the scoured areas between Ices Ferry and the new U.S. 48 bridges where silt deposition occurs downstream of the U.S. 48 bridge (Fig. 3). Likewise, depths at Ices Ferry bridge have changed from an original bottom depth of 16.5 m in 1921 to 13.7 m in 1945 to 7.0 m in 1990 (Fig. 3), while depths at the U.S. 48 bridge have varied from 11.5 m in 1929 to 7.6 m in 1972 to 6.2 m in 1990. Today as much as 9 m of mud is evident at the Ices Ferry bridge area.

Bottom depths from Sunset Beach to the dam are deeper today than in 1956 (Fig. 3). Note that depths at old transects 49 and 64 (A) are 6 m and 5.4 m deeper today than in 1956 (Fig. 3). Also the greatest depth in 1956 was 30.4 m near the dam, while in 1990 the deepest point is located along the safety zone warning line approximately 109 m from the west shore at 32.3 m. The average depth across old (A) transect 64 today is 17.9 m.

Rubbles Run is the deepest of all the tributaries entering Cheat Lake and possesses depths of 19.9 m just inside its mouth and upriver to the bend near the old, still extant but unused, iron bridge. Maximum depths of the Sunset Beach tributary and harbor area are 8.9 m. A large mud flat with a stream running down its length is exposed during low water or November drawdowns.

Greatest widths across Cheat Lake have remained unchanged at approximately 1,094 m at Sunset Beach and the 1956 transect 50 (A). Widths of 1,021.4 m (3,360 ft.) exist south of Ices Ferry and at the new U.S. 48 bridge. The widest lower lake area occurs at the level of Morgan Run (1,030.5 m). If one includes a 152 m cove, a width of 1,741.9 m or a little over a mile exists on the Grammy's Run transect (Fig. 1). Maximum silt or mud accumulation areas of 13.7 m are also evident near Canyon and at the dam (B, Fig. 3).

DISCUSSION

Few have had or taken the opportunity to note and review the effects of filling in or the fate of a dam and its water depths once constructed. What seemed to be a natural filling in process at Cheat Lake has now been shown to have been drastically altered, probably by the three day 3–5 November 1985 flood whose waters equaled or exceeded the flows recorded in 1888 (Cong. Rec., 1942). For the moment, the power company operating the dam at Cheat Lake has been spared worry of the lake's continued filling in. However, new plans by the state to begin a massive upriver timber effort and to stimulate land development use may yet return Cheat Lake to its long-term end of filling in.

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REFERENCES CITED

BURLEY, J. W. A. 1955. Studies concerning the decline of aquatic life in Cheat Lake. An investigation of algal deficiencies. M.S., Univ. W. Va. 48 pp.

CALLAHAN, J. M. 1923. History of West Virginia Old and New in One Volume. Vol. 1. Historical, Am. Hist. Soc., Chicago, IL. 723 pp.

CARPENTER, L. V., AND L. K. HERNDON. 1928. Report of Pollution Study in the Cheat River Basin, West Virginia. W. Va. St. Water Comm., 46 pp.

———, AND ———. 1930. Report to the State Water Commission on Recovery of the Cheat River Basin. W. Va. St. Water Comm. 19 pp.

CONGRESSIONAL RECORD. 1942. Cheat River and its tributaries in West Virginia. 78th Congr. 2nd Session. H.D. 645:1–96, plates 1 & 10.

CORE, E. L. 1959. Biological Investigations of Cheat Lake (Summary). W. Va. Univ., Morgantown. 39 pp.

GROVER, N. C., AND S. LICHTBLAU. 1937. The Floods of March 1936. Pt. 3. Potomac, James and Upper Ohio Rivers. U.S. Geol. Surv. Water Supply Pap. 800, 351 pp.

MORELAND, J. R. 1940. The Early Cheat Mountain Iron Works. W. Va. Univ., Morgantown. 340 pp.

SCHWARTZ, F. J. 1956. The Cheat River Basin: Past, Present, and Future. W. Va. Univ., Morgantown. 145 pp.

U.S. DEPT. COMMERCE WEATHER BUREAU. 1955. Climatological data for West Virginia. Ann. Surv. Vol. LXII No. 3; 156–163.

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The conceptual relationship between ontogeny and phylogeny

William L. Fink

Abstract.—Studies of ontogenetic processes are fundamentally dependent on hypotheses of phylogeny. The model of Alberch et al. (1979) is reformulated in terms of phylogenetics and used to describe how heterochronic ontogenetic processes can be detected in nature. Heterochronic processes producing paedomorphosis can result in morphologies which resemble primitive (retained ancestral) traits; the conditions under which paedomorphic and primitive features can and cannot be distinguished are described. The utility of ontogeny for determination of evolutionary character transformations and character polarity and for detection of convergence and parallelism are considered. The ontogenetic criterion for assessing polarity is independent of hypotheses of phylogeny and may be as effective as outgroup comparison. Ontogenetic analysis may aid in the detection of convergence but not in the detection of parallelism.

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I. Introduction

One avenue towards the elucidation of evolutionary mechanisms that has recently received much attention is the study of ontogeny. This renewed interest in ontogenetic phenomena is a response to the failure of classical population genetics alone to account for evolutionary diversity. Reassessment and refinement of early evolutionary models emphasizing the importance of development, and a synthesis of these models with those of population genetics, promise to provide fundamental new insights into the study of the origins of morphological and phylogenetic diversity.

Most recent research concerning ontogeny (e.g., Løvtrup 1974; Gould 1977; Alberch et al. 1979) attempts to apply evolutionary explanations to observed patterns of morphology and morphological change. As one reads this literature, it becomes apparent that the study of ontogeny is considered a special tool in the study of evolution. One systematist (Nelson 1973) even suggests ontogeny to be an independent criterion for the evaluation of evolutionary transformations. Other authors have touched upon the problems that some forms of ontogenetic development, particularly neoteny, pose for systematic analysis (Eldredge and Cracraft 1980; Wiley 1980). My purpose here is to delimit more clearly both the assumptions underlying ontogenetic research as it is applied to evolutionary biology and the implications of this research for systematic biology.

II. Detection of Heterochrony

A major focus of recent ontogenetic work is heterochrony. Briefly, changes in developmental rates or timing and their epigenetic consequences are suspected of being instrumental in the acquisition of evolutionary novelties, including those often major changes associated with large scale cladal diversity. The two general forms of heterochrony thought most likely to be associated with such diversity are paedomorphosis, traditionally defined as a process that produces a descendant with adult morphology similar to juvenile morphology of an ancestor (see Gould 1977) and peramorphosis, production of descendants whose form transcends that of an ancestor (Alberch et al. 1979). Although Gould (1977) and Alberch et al. (1979) discuss at length various heterochronic processes and methods by which the morphological results of such processes might be described, they do not provide explicit descriptions of the procedure for detecting those results in nature. This omission may reflect the focus of these authors on evolutionary process, per se, but it leaves unexplicated a significant problem. Heterochrony is discussed by these authors in the context of "an-

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On the relationship of the myotome to the axial skeleton in vertebrate evolution

George V. Lauder, Jr.

Abstract.—The traditional belief that vertebrae must alternate in position with the segmented body musculature (myotomes) to allow bending of the axial skeleton is evaluated in terms of the patterns of development and structure of gnathostome vertebrae. The key functional parameter allowing lateral bending of the axial skeleton is the intersegmental position of both the neural and haemal arches, not the centrum. The intersegmental position of both the centrum and arches in tetrapods is the result of a secondary association of the centrum with the primary intersegmental position of the neural and haemal arches. The pattern of vertebral ontogeny and structure in primitive gnathostomes suggests that a causal link between sclerotomic resegmentation during amniote development and the presence of intersegmental vertebrae in the adult is spurious and corroborates the hypothesis that the process of resegmentation evolved as a method of redistributing large volumes of sclerotome cells during development. Patterns of vertebral construction in lower vertebrates are related to fast-start performance and the use of the body as a hybrid oscillator during locomotion.

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Introduction

Vertebral structure has traditionally been the dominant criterion by which early tetrapods, particularly the Amphibia, have been classified. Vertebral structure in these early forms is highly complex and a correspondingly intricate terminology has developed to describe the anatomy and evolution of the axial skeleton.

Williams (1959) attempted to clarify the terminological confusion by showing that the Gadovian system of vertebral classification, based on the hypothesis that vertebral form was the result of various combinations of embryonic arcualia (Gadow's basidorsals, basiventrals, interdorsals, and interventrals) had no embryological basis. In no vertebrate did Gadow's arcualia appear during ontogeny. Williams' suggestion that this terminology be abandoned in favor of a more embryologically accurate one has been generally accepted and his review has greatly stimulated investigation into patterns of vertebral ontogeny and evolution.

In recent years a number of studies (Andrews and Westoll 1970b; Panchen 1967, 1977; Parrington 1967, 1977) have considered the functional basis for vertebral structure and although some limited success has been achieved (Andrews 1977; Panchen 1977) essentially no testable hypotheses have been generated linking vertebral structure to function, especially in lower vertebrates. In addition, the role of sclerotomic resegmentation in the evolution of tetrapod vertebrae is a matter of some debate (see Schaeffer 1967; Wake 1970; Williams 1959), and yet assumptions underlying hypotheses of sclerotome cell movement during ontogeny frame current conceptions of vertebral homology (see Laerm 1979a).

In spite of several recent reviews of vertebral evolution (Panchen 1977; Schaeffer 1967; Wake 1970) the functional interrelationships of the myotome to the vertebra have not been explicitly treated and the tremendous variation in lower vertebrate vertebral structure has not been used to test hypotheses of the function of sclerotomal resegmentation in tetrapods.

The purpose of this brief review is twofold: (1) To examine the diversity of vertebral structure in lower gnathostomes as a basis for a re-

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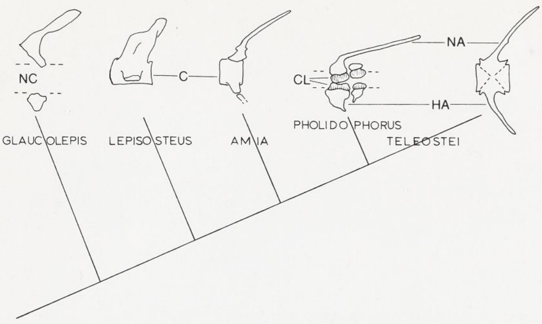

FIGURE 1. Patterns of vertebral structure in some actinopterygian fishes. Anterior is to the left, vertebrae are seen in lateral view, and dashed lines indicate the width of the notochord. Abbreviations: C, centrum; CL, notochordal calcifications; HA, haemal arch and spine; NA, neural arch and spine; NC, notochord. *Glaucolepis* from Nielsen (1942), *Amia* from Schaeffer (1967), and *Pholidophorus* from Patterson (1968).

consideration of the significance of sclerotomal resegmentation and as a guide to reinterpreting the primitive functional association between the myotome and the axial skeleton, and (2) To generate first-order hypotheses relating the occurrence of central ossifications in lower vertebrates to locomotor mode. I will attempt to synthesize some recent studies on fish locomotion with patterns of vertebral structure and indicate how future studies might profitably examine the functional significance of vertebral structure in lower vertebrates.

Patterns of Vertebral Structure

I will not exhaustively review vertebral development but only point out key developmental and structural aspects relevant to a consideration of vertebral function.

Primitive gnathostome vertebrae.—While the process of sclerotomal resegmentation to form the definitive centrum has been well established in amniotes (Hall 1977; Williams 1959), there is no evidence that resegmentation plays any role in the development of the teleost centrum (Francois 1966; Laerm 1976).

Within the Teleostei, vertebral embryology and form are remarkably consistent. Initially a perichordal tube is formed from sclerotomal cells by the medial migration of these cells to form a continuous layer over the notochord and its sheath, the elastica externa (Farugi 1935; Laerm 1976). Another membrane layer then differentiates between the externa and the internal notochordal epithelium, the elastica interna. Sclerotomic cells are not arranged metamerically around the notochordal membranes.

The notochordal sheaths then begin to thicken in (ultimately) intervertebral positions causing a depression between the thickened areas. In these depressions centrum development begins. The characteristic amphicoelous shape of the teleost centrum is due to the expansion of the notochordal sheath at the ends of the presumptive centrum and the direct ossification of sclerotomal tissue which essentially molds itself around the biconical expanded sheath.

The centrum always ossifies directly from two main centers (Francois 1967; Laerm 1976; Schaeffer 1967) while the neural and haemal arches are preformed in cartilage and subsequently ossify.

A key feature of teleost vertebral development is that the neural and haemal arches need not always be associated with the centrum in a fixed manner. Although in teleosts the arches consistently maintain their association with intersegmental myosepts, they may have a variable relationship to the centra (Farugi 1935). Anteriorly, for example, the neural arch may attach to the anterior of the centrum while in the caudal region it may attach posteriorly. In some forms (*Amia*) the position of the centrum may even be intrasegmental (Schaeffer 1967), the myosepts passing *between* adjacent vertebral centra to attach to the arches. The adult centrum may thus have a variable relationship to the myosept even along the axial skeleton of a single individual.

This pattern is more widespread in non-teleost actinopterygians, the halecomorphs and chondrosteans, where a diplospondylous condition occurs frequently in the caudal region (Nielsen 1942; Patterson 1968) and notochordal calcifications (centra are absent in most groups, Fig. 1) may or may not align with the myosepts.

In primitive ray-finned fishes the notochord is unrestricted and the neural and haemal arches rest on it. In palaeoniscoids (Nielsen 1942) the neural arches were paired and were not fused in the midline dorsally but were probably held together by fibrous connective tissue. Ventrally, the haemal arch elements (basiventrals

Electrophoretic identification of raw and cooked fish fillets and other marine products

*C. P. KEENAN and J. B. SHAKLEE**

Fish fillet identification usually involves the separation of soluble muscle proteins by electrophoretic methods. An electrophoretic methodology has been developed that allows the identification of both raw and cooked fillets. The procedure is simple, inexpensive and at least as sensitive as isoelectric focusing. Using barramundi (*Lates calcarifer*) as a model, numerous variables, such as size and sex of fish, method and duration of storage, conditions of sample extraction, protein concentration in extract and cooking of fillet, have little effect on the ability to identify the fish. Each of the over 50 fish species tested exhibited a unique electrophoretic pattern that allowed unambiguous identification. This was also true for groups of closely related fish species and for numerous invertebrates tested.

When fish muscle is cooked not all proteins are denatured. On the basis of their distinctive UV absorption spectra, low molecular weights, approximate isoelectric points and subunit structure, the predominant heat-stable proteins ideal for identifying both raw and cooked fillets have been identified as parvalbumins.

Supply and marketing problems involving substitution and/or mislabelling have been documented for many edible biological products, e.g. scallops vs ray vs shark, beef vs kangaroo vs horse, varieties of cereal grains such as wheat strains, etc. The problem is particularly pronounced when dealing with processed products, such as fillets, mince, steaks and flour, which lack the external morphological characters commonly employed to identify species. Recently there have been numerous problems in Australia associated with the marketing of fish fillets, particularly those of the highly prized barramundi (*Lates calcarifer*) in the wholesale and retail markets and at restaurants (Anon. 1982a, b, Sumner & Mealy 1983). For the most part these problems have involved the substitution or mislabelling of fillets from 'less desirable' species for those of 'more desirable' species. This situation clearly points to the need for a reliable and efficient procedure to identify the species of origin of fillets and other processed products to ensure the correct labelling of commercial products and thereby provide consumer protection. Such a procedure could also be used for inspection purposes to test imports and/or exports and provide a means of monitoring fisheries to enable enforcement of closed seasons such as the seasonal closure of the barramundi fishery in northern Australia.

Electrophoresis of water-soluble tissue proteins is a technique which has been used in intra and inter specific studies in fisheries biology for many years (Utter, Hodgins & Allendorf 1974, Avise 1975, Ihssen *et al.* 1981, Shaklee, Tamaru & Waples 1982, Shaklee 1983). As a means of species identification, electrophoresis has two main strengths. First it often provides clear, qualitative discrimination among morphologically indistinguishable species. Second, it can be used to estimate quantitatively the degree of genetic relatedness among species. In addition to the obvious role of electrophoresis in basic taxonomic and systematic investigations, the technique has tremendous potential in applications such as product identification and inspection. The uses of electrophoretic and other biochemical techniques for species identification in an inspection context have been many and varied (reviewed by Mackie 1980, Kurth & Shaw 1983). In many cases this is a reflection of the continuing development of new procedures and resulting changing 'recommended methods' of the [US] Association of Official Analytical Chemists (AOAC) (e.g. Thompson 1960, 1967, Learson 1970, Lundstrom 1980, 1983a) and of similar bodies elsewhere (e.g. Mackie 1969, 1972, Royal Australian Chemical Institute, etc.).

In Australia many different biochemical techniques are currently being employed to identify processed food products (Kurth & Shaw 1983). Agarose isoelectric focusing (IEF) is one method being used for identifying fish fillets (Anon. 1982b, Hamilton 1982). Different red meat species are identified using either polyacrylamide or agarose IEF with general protein staining as well as electrophoresis on cellulose acetate membrane strips with subsequent enzyme staining (Sinclair & Slattery 1982, Slattery & Sinclair 1983). Bremner and Vail (1983) have used disc polyacrylamide gel electrophoresis (PAGE) for the identification of fish species and Wrigley, Autran & Bushuk (1982) have used gradient PAGE to identify wheat grains and fish species (Wrigley, pers. commun).

One of the simplest and most cost effective methods of identification so far developed has relied on immunological precipitation (Swart & Wilks 1982) for the detection of red-meat substitution. However, this procedure is not effective in detecting substitution of closely related species, e.g. sheep and goat, cattle and buffalo, horse and donkey (Swart & Wilks 1982). Furthermore, this approach has severe limitations when the number of possible species is very large as is the case with fishes. The limitations stem from the difficulties associated with: producing antisera for tens or hundreds of different species; testing each sample with all possible antisera to obtain a positive identification; and perhaps most important obtaining antisera specific for each fish species to be identified.

Recent advances in electrophoresis and protein staining techniques have resulted in improvement in the quality of gels and their results. We have used a thin (0.8 mm) and large (approx. 200 mm x 260 mm) polyacrylamide slab gel for our general protein experiments, based on the method of Gahne, Juneja & Grolmus (1977). The use of a slab gel allows side-by-side comparisons of 25–45 samples under identical conditions, a distinct advantage over

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disc polyacrylamide gels (cf. Bremner & Vail 1983, Lundstrom 1983b). Side-by-side comparisons are desirable as comparisons between separate gels can be unreliable (Ferguson 1980) unless considerable care is taken to standardise each gel. Minor variations of pH, ionic strength, gelling time and temperature, and running conditions can alter protein mobilities. We have used a high pH discontinuous buffer which causes virtually all muscle proteins to migrate anodally into the separation gel, separates small, highly charged proteins from the buffer front, and increases the resolution of individual proteins by sharpening each zone. The increased resolving power of this procedure for general muscle proteins is due to the large size of the polyacrylamide gel, the high resolution of the buffer system and the sensitivity of the two general protein stains used, viz. Coomassie blue and a silver staining technique (modified from Merril, Goldman & van Keuren 1982). The latter allows detection of nanogram amounts of protein. The companion approach, starch gel analysis of specific enzymes in muscle tissue, is similarly robust due to the high resolving power of starch gels for specific enzymes, the large numbers of buffer systems and enzyme stains which can be accomplished using this medium to optimise the resolution of each enzyme system, and the relatively simple banding patterns resulting from specific enzyme staining which make genetic interpretations of the biochemical phenotypes relatively straightforward.

It is now generally recognised that most species of organisms exhibit significant levels of genetic polymorphism. As summarised by Selander (1976), approximately one-third of the gene loci screened in fishes are polymorphic at the 1% level while by this criterion more than one-half of the loci screened in invertebrates are polymorphic. The significance of these observations to the problem of fish fillet identification is obvious. As individuals within a species may express different allelic forms of a protein or a specific enzyme due to genetic polymorphism, reliable species identification can require a statistical assessment based upon knowledge of the qualitative nature and quantitative aspects of such polymorphisms. If such knowledge is not available, individuals of the same species could be mis-identified as members of two or more different species because of one or more differences in their protein banding patterns. Theoretically, it is also possible that two different species could share polymorphisms that might lead to mis-identification as members of the same species, although this result is much less likely than the former. In order to avoid such mis-identifications, fish fillet identification by electrophoresis should be based upon genetic interpretations of the protein or enzyme banding patterns. This may involve the screening of numerous specimens (from diverse localities if possible) to identify and quantify the types and amounts of variation (both genetic and non-genetic) in banding patterns characteristic of each species of interest.

This paper demonstrates the usefulness of the techniques for distinguishing between products of vertebrate (fish) or invertebrate origin and for identifying the precise species of origin from which a product was taken. Even commercially-cooked fish muscle can be readily identified as to the species of origin using our electrophoretic procedure by analysing the heat-stable parvalbumins present in fish muscle extracts. The techniques described are simple and inexpensive, require minimal specialised equipment and constitute a sensitive and reliable method of species identification for both vertebrates and invertebrates.

Materials and methods

Samples

Specimens were shipped frozen to the CSIRO Marine Laboratories at Cleveland, Qld and were stored at –20°C until used. Samples of fresh fish, fish fillets and other seafood and of commercially-cooked seafood products were obtained from local commercial sources in the Brisbane area. The fresh samples were either used immediately or stored at –20°C until analysed. In nearly all cases, intact specimens were identified using one or more common references (e.g. Munro 1967, Grant 1978, Grey, Dall & Baker 1983) to ensure correct species identification.

Extract preparation

Samples of skeletal muscle were dissected from intact fish specimens or isolated fillets and homogenised with a motorised pestle in an equal amount (w/v) of buffer (0.1 M Tris, 0.001 M EDTA and 5 x 10^{-5} M $NADP^+$, adjusted to pH 7.0 with HC1; Selander *et al.* 1971) unless otherwise specified. Whenever possible care was taken to minimise the content of red muscle fibres usually associated with the lateral line in the muscle sample. This was done to standardise the sampling procedure and simplify subsequent interpretation since red and white tissues are known to be biochemically distinct and exhibit different enzyme and protein profiles (e.g. Sharp & Pirages 1978). Extracts of muscle or other tissues from the various invertebrate species were prepared in a similar manner. The homogenates were then centrifuged at 20 000 x g for 30 min at 4 °C. Supernatants were pipetted into individually labelled glass vials and stored capped at –70°C, except in experiments designed to investigate the effect of storage temperature on extracts.

Specific enzyme analyses

Horizontal starch gel electrophoresis was performed at 5°C using the general procedures of Selander *et al.* (1971) with minor modifications. The specific details of the techniques used are described in Shaklee and Keenan (1985). Connaught starch (lot 380–2) at 120 g/L was used throughout the study. Two electrophoresis buffers were used in this investigation. The TC–1 buffer was equivalent to buffer 1 of Shaw and Prasad (1970) while the CAAPM (citric acid, aminopropylmorpholine) pH 6.0 buffer was according to Clayton and Tretiak (1972). Specific enzyme histochemical staining was accomplished after electrophoresis using the recipes of Shaw and Prasad (1970), Siciliano and Shaw (1976) and Harris and Hopkinson (1976) with minor modifications. Enzyme names and Enzyme Commission numbers follow the recommendations of the Commission on Biochemical Nomenclature (1973). Isozyme banding patterns were interpreted using existing literature on molecular structure, genetics and observed electrophoretic variation of enzymes (Shaklee 1983). Band positions (as distance travelled from the sample origin) were measured to the nearest 0.5 mm. Control extracts of barramundi muscle were run on each gel. Relative mobilities (Rms) of the isozymes of various fish species were calculated using the mobility of the presumably homologous isozyme in barramundi as a reference. For invertebrates, Rms were again calculated using the barramundi enzyme as a reference although homology has not been inferred in this case. Negative values of relative mobility refer to enzymes exhibiting cathodal migration.

General protein analyses

Thin (0.8 mm) slab polyacrylamide gel electrophoresis (PAGE) was used to separate the muscle proteins of the supernatant. The specific details of the techniques used are described in Shaklee and Keenan (1985). The gels consisted of 10% acrylamide (+0.25% bisacrylamide) in the anodal running gel (235 mm long), 4% acrylamide (+0.1% bisacrylamide) in the sample application zone (20 mm long), and 8% acrylamide (+0.2% bisacrylamide) in the cathodal portion of the gel (40 mm long). The general configuration of the gels was similar to that described by Gahne *et al.* (1977). We used a discontinuous LiOH buffer system (lithium hydroxide, boric acid/Tris, citric acid) modified from Selander *et al.* (1971). Final buffer concentrations were 0.03 M lithium hydroxide, 0.1925 M boric acid (pH 8.2) for the electrode; and 0.003 M lithium hydroxide, 0.01925 M boric acid, 0.046 M Tris, 0.00685 M citric acid, 0.0375% mercaptoethanol (pH 8.4) for the gel.

Samples were applied with filter paper wicks. Electrophoresis was carried out in a refrigerator at 5°C until the bromophenol blue tracking dye in the buffer front had migrated approximately 200 mm into the 10% gel. Separation took 6 h at 500 V or, if a cooling plate was used, 3 h at up to 1500 V and 40 mA maximum current. After electrophoresis, the 10% anodal portion of the gel was immediately stained with Coomassie blue (Shaklee & Keenan 1985). When greater sensitivity was required, Coomassie-stained gels were subsequently fixed and destained overnight and stained using a modified method of the silver technique of Merril *et al.* (1982) according to Shaklee and Keenan (1985). Because preliminary experiments failed to reveal a protein having cathodal electrophoretic mobility under the conditions used, only the anodal 10% separating gel was stained for protein in the PAGE experiments. Protein banding patterns were recorded by measuring the

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Speciation and Evolution of Marine Fishes Studied by the Electrophoretic Analysis of Proteins[1]

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ABSTRACT: Electrophoretic analysis of proteins can be utilized to clarify the taxonomic status of species as well as the evolutionary interrelationships of populations, species, and higher taxa. Electrophoretic data for over 50 gene loci in the bonefish *Albula "vulpes"* (Albulidae) demonstrate the existence of two discrete species in Hawaii and throughout the Indo-West Pacific. Similar studies of lizardfishes (Synodontidae) in the genera *Synodus* and *Saurida* reveal that several unreported and/or undescribed species occur in the Hawaiian Islands. Both of these studies emphasize the power of electrophoresis in distinguishing morphologically cryptic species. The interrelationships of species and genera of lizardfishes and of goatfishes (Mullidae) were investigated by using values of genetic distance derived from protein similarities and differences. These comparisons and the analysis of the two bonefish species, provide additional examples of the basic independence of the rates of biochemical and morphological evolution.

Published electrophoretic investigations of fish speciation and evolution are reviewed and several guidelines for future applications of the technique are proposed. The importance of sympatric samples, the use of large numbers of gene loci, and the conservative interpretation of genetic distance values are emphasized. The utility of electrophoretic data for (*a*) identifying species (especially juvenile, larval, and embryonic stages, or isolated animal products such as fillets); (*b*) identifying F_1 interspecific hybrids; and (*c*) estimating absolute and relative divergence times between taxa are discussed. Finally, the combined use of electrophoretic data from fresh specimens together with multivariate morphometric analyses of both the fresh specimens and preserved museum type specimens is recommended as a robust approach for sorting out nomenclatural problems.

FOR GONOCHORISTIC, SEXUALLY REPRODUCING organisms such as most fishes, the species concept is based upon the reproductive isolation of groups of true-breeding populations from other such groups. In practice, species are nearly always distinguished and described on the basis of anatomical differences. It is reasonable to expect that nearly all currently recognized species should be morphologically distinct from one another, given this practice.

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However, anatomical differentiation is neither a necessary nor a sufficient basis for the recognition of separate species. The literature is filled with examples of species that exhibit dramatic anatomical polymorphisms yet are conspecific and with examples of morphologically cryptic species complexes that are, in fact, independent genetic units (Borden et al. 1977, Gould, Woodruff, and Martin 1975, Grassle and Grassle 1976, Salmon et al. 1979).

An alternative criterion for the recognition of distinct species—that of actual reproductive isolation—seems obvious given the above definition of species. However, this criterion is weakened by the numerous examples of occasional interbreeding between well-accepted species. Indeed, such interspecific hybridization under laboratory and/or natural field conditions is well documented for fishes (Schwartz 1972, 1981) and other groups of animals.

The technique of gel electrophoresis of proteins provides a powerful, although indirect, test of the validity of presumed species. Because this technique allows the measurement of genetic relatedness among individuals (due to the codominant expression of most alleles at protein-coding loci), it can serve as a means for determining the genetic uniqueness of any set of organisms (i.e., identifying distinct species). The approach is particularly robust in cases of true sympatry (in space and time). In such cases, genetically differentiated species are easily recognized when fixed allelic differences are detected. Populations that are sympatric and characterized by fixed allelic differences have clearly evolved effective means of reproductive isolation. Such populations must therefore be considered true biological species. On the other hand, observations of genetic uniformity, either in terms of similar allele frequency distributions among samples or especially in terms of invariant loci identical in all individuals, are consistent with, but do not definitively establish, the conspecific nature of populations (but see Graves and Rosenblatt 1980, Manooch et al. 1976, Sage and Selander 1975, Turner and Grosse 1980).

In cases of allopatry (in space or time), the above distinctions become blurred due to the potentially confounding effects of geographic or temporal differences in the allelic composition of organisms. Geographically, this may take the form of apparent clines in allele frequency or, given discontinuous sampling in space or time, may even appear as apparent fixed allelic differences among samples (Aspinwall 1974, Powers and Place 1978). Extreme care must therefore be exercised in interpreting such data for allopatric samples, because reproductive isolation resulting from spatial or temporal allopatry may not have any biological basis. It is, at best, very difficult to determine whether allopatric populations would or could freely interbreed if contact were restored under natural conditions.

Besides providing a robust measure of the reproductive relationships of sympatric populations, the electrophoretic approach yields additional benefits. One is the unambiguous identification of interspecific F_1 hybrids between two species having multiple fixed allelic differences. This is a direct result of the codominant expression of alleles characteristic of protein-coding loci and is a clear improvement over the use of morphological criteria which are generally less powerful due to the quantitative (blending) inheritance of most anatomical characteristics. A second benefit of the biochemical analysis of species derives from the molecular clock hypothesis (Maxson and Wilson 1974, Nei 1971), which assumes that proteins evolve at relatively constant rates. Thus, by appropriate calibration, it is possible to estimate the approximate time of divergence of any two species (or higher taxa) based on values of genetic distance derived from electrophoretic studies.

This paper describes our electrophoretic investigations of three groups of inshore marine fishes and provides some general guidelines concerning the application of electrophoresis to studies of speciation and evolution.

MATERIALS AND METHODS

Fish specimens were obtained by field capture or by purchase from commercial sources. All animals were stored frozen at −20°C until used. Methods of sample preparation, gel

Isozymes: Current Topics in Biological and Medical Research
Volume 11: Medical and Other Applications 213–247

The Utilization of Isozymes as Gene Markers in Fisheries Management and Conservation

James B. Shaklee

Division of Fisheries Research, CSIRO Marine Laboratories, 233 Middle Street, Cleveland, Queensland 4163, Australia

I. STOCK STRUCTURE ANALYSIS

At present, the most widely accepted definition of a species (as applied to sexually reproducing forms) is that of a group of self-reproducing organisms which can and do interbreed among themselves but are reproductively isolated from other such groups. A natural consequence of the reproductive independence of separate species inherent in this definition is the expectation of progressive genetic differentiation between species eventually leading to the development of numerous qualitative differences between such taxa. Although the above definition of a species implies interbreeding and thus genetic continuity within the taxon, it is generally recognized that most species do not behave as simple panmictic groups. Indeed, theoretical considerations of the magnitude of a species' geographic range relative to the mobility of individuals and the existence of geographic and environmental barriers which are expected to reduce or prevent gene flow between individuals in different areas together with direct observations of patterns of intraspecific variability in morphological, physiological, and biochemical traits have long been recognized as evidence for nonrandom reproduction within species. This genetic heterogeneity within species is generally explained by the existence of demes or subpopulations, each of which represents a self-sustaining panmictic breeding unit within the species. If the amount of differentiation between such groups is great enough, they may be afforded formal taxonomic status as discrete subspecies but, more often, they are referred to as demes, races, or (in the case of commercially exploited species) stocks. Because the management of fisheries depends upon continued successful reproduction of individual stocks, the existence of such a subpopulation or stock heterogeneity within a species has direct relevance to the formulation of harvest and/or conservation practices.

The electrophoretic analysis of protein variation within a species, because it can provide more or less direct information regarding the genetic interrelationships of populations throughout the species' range, has been applied to the study of stock structure in numerous aquatic organisms. The procedure depends upon the characterization of each sample or population in terms of its allele frequency distributions at several polymorphic loci and the statistical analysis of these data relative to the null hypothesis that all samples are drawn from a single large panmictic group and therefore should have similar allelic frequencies. In almost all cases, the chi-square statistic (or a variation of it) is utilized although analysis of variance has recently been suggested as a more appropriate test [Gauldie and Johnston, 1980]. Problems in the application of this approach fall into three general areas: (1) adequate detection of genetic variation, (2) correct interpretation of observed variation, and (3) proper experimental design and statistical analysis. The consideration of several published studies will serve to emphasize the nature of some of these problems.

A. American Lobster (Homarus americanus)

Genetic aspects of population structure in the American lobster off the Atlantic coast of southern Canada and the northeastern United States were investigated by Tracey and co-workers [Tracey et al, 1975]. The three major

Précis de Zoologie: vertébrés. 2. Reproduction, biologie, évolution et systématique. Agnathes, poissons, amphibiens et reptiles

By Pierre-P. Grassé. 1976. (Masson, Paris, New York, Barcelone, Milan. 2nd ed. 464 pp., illus. (no price given).

This is the middle volume in a series of three, the first being on invertebrates, the third on birds and mammals. They are intended to be compact up-to-date texts for students and laymen, especially those interested in environmental biology.

The first 130 pages discusses embryology of all the classes of vertebrates, not just fish, amphibians, and reptiles. The tone is descriptive without theoretical and experimental discussions or descriptions of abnormalities. The sections on fertilization, cleavage, and gastrulation are well written and current and that on embryonic membranes and placentation is very thorough. The origin of germ cells and development of gonads are treated in depth. But here detailed description stops, and development of such organs as the eye, ear, heart, and kidneys is described sketchily, if at all.

In the second part the classes of vertebrates are discussed one by one from the lampreys up through the reptiles. The organization of the material is loose, but includes evolution, anatomy, physiology, reproductive biology, and descriptions of some families in each group.

The remainder of the book is divided between fishes (110 pages), amphibians (77 pages), and reptiles (113 pages). Aside from five citations for consultation, there is no list of references. A detailed index is provided.

The section on fishes is a mixture of old and new. Much of the classification evidently derives from the 1958 Traité de Zoologie, Tome 13. Unfortunately the order Tetraodontiformes is still retained amongst the soft-rayed fishes between the Clupeiformes and the Cypriniformes, rather than amongst the spiny-rayed fishes, despite considerable evidence to the contrary. The Cyprinodontiformes and Beloniformes are not united under the Atheriniformes, nor are the Gonorhynchiformes recognized with the Cypriniformes in a superorder Ostariophysi, although there is good support for such a grouping. It would have been preferable to place the Acanthodii nearer the Elasmobranchii and Osteichthyes, rather than before the Placodermi to express better their close relationship with the latter. In short, the recent advances in the higher classification of fishes have not been reflected in classification used.

On the other hand, new information on the pseudobranch (up to 1975) and on electroreceptors (1974) has been incorporated. P.W. Webb's work (1975. Bulletin of the Fisheries Research Board of Canada Number 190) was probably not available at the cut-off date but might otherwise have been referred to in the section on locomotion. The coelacanth, *Latimeria chalumnae*, is treated in interesting detail and provides an excellent summary of anatomical information.

The small type and narrow page margins permit a great deal of information to be packed into some 450 pages. The drawings, editing, and binding are up to the usual high standards of Masson. We personally would prefer matte to the glossy paper which is hard on the eyes.

Although not an exhaustive treatment of reproduction, biology, evolution, and systematics of vertebrates the volume does provide a useful summary in a concise, clear, and well-illustrated format.

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BOOK REVIEW

Development of Fishes of the Mid-Atlantic Bight. An Atlas of egg, larval and juvenile stages

BY DANIEL J. FABER AND DON E. MCALLISTER

Volume 36 • Number 6 • 1979

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Service des pêches et de la mer

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LEXIQUE ANGLAIS — FRANÇAIS

Termes techniques à l'usage des biologistes

ÉDITIONS DE L'UNIVERSITÉ D'OTTAWA
Ottawa, K1N 6N5 (Ontario), Canada
1978

427 pages - plus de 10,000 entrées - $12.00

Lexique anglais-français, Termes techniques à l'Usage des Biologistes

By Jean Vaillancourt. 1978. Editions de l'Université d'Ottawa, Ottawa. 427 pp. Paperback $12.00.

Biologists, like the animals they study, must look beyond linguistic and national boundaries, to be aware of developments in their field. This lexicon, of a high degree of completeness, will help the biologist reap the full benefits of discoveries in two of the world's most important languages.

The lexicon consists of two principal parts. The first and largest is an English-French lexicon with the entries listed alphabetically in English and numbered consecutively. The emphasis is thus on providing the equivalent word in the other language rather than a definition. The second section is an alphabetical index of French terms keyed by number to the first section. This approach permitted condensation of the text and reduction in cost without loss in utility.

The English-French lexicon is laid out in the following manner: the English word in boldface type, which permits the word to be easily picked out, followed by one or more classificatory abbreviations such as Anat., Biol., Zool., Océanogr., Méd., Bot., Ichtyol., Ornith., Micr., etc.; the French synonym or synonyms; the plural form (only when irregular); and the gender.

The only other even roughly comparable sources the reviewer is aware of are the following: *Glossaire de biologie animale* by Roger Husson (1970, Gauthier-Villars, Paris), which is unilingual and gives about 2500 definitions; the *Dictionnaire français-anglais, anglais-français des termes médicaux et biologiques* by Pierre Lépine and Philip R. Peacock (1974, Flammarion, Paris), having some 6500 words; and the *Dictionary of biology* by Günther Haensch and Giselin Haberkamp de Anton (1976, Elsevier Scientific Publishing Company, Amsterdam), with synonyms in four languages for about 9800 terms. (There are also a number of unilingual English biological dictionaries.) None of these give comparable coverage. To check the thoroughness of coverage the first 25 biological terms found in the preceding dictionaries were checked to see whether they were included in Vaillancourt's lexicon. Of the 25 terms in all three, about 90% were found in Vaillancourt. The reviewer has a rather specialized manuscript dictionary of ichthyology. Even in this case about half these specialized terms were found in Vaillancourt. The coverage is clearly very good. Over 10 400 terms are included.

The disciplines covered include bacteriology, botany, zoology, marine biology, anatomy, systematics, evolution, ecology, limnology, oceanography, genetics, paleontology, pharmacology, and physiology as well as related terms in geology and geography.

In a discipline as broad as biology it would be impractical to include every term. Only a few omissions were noted — neotype (néotype), meristic (méristique), and ray in the sense of fin ray (rayon), although ray in the sense of a kind of fish was included. Ichthyologist and fish(eries) biologist are equated, although in general use the first is usually restricted to the theoretical student of systematics, anatomy, evolution, ecology, and zoogeography of fishes, as opposed to the applied management of fishes; however, these are minor points.

I wholeheartedly recommend the addition of this book to your biological library. There have been many times that I wished I had a comparable authoritative source book. Vaillancourt is to be congratulated for his breadth of coverage which will make it invaluable for the student and professional.

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Fisheries History Section

NEWSLETTER

1997, No. 2 (August) Mark R. Jennings and John R. Moring, Co-Editors

PRESIDENT'S MESSAGE

The AFS Annual Meeting in Monterey promises to be an enjoyable location and time to hold a scientific meeting. It may be the largest registration for any AFS meeting with approximately 1100 papers presented. I am guessing that many Fisheries History Section members will be attending.

I want to encourage all of you to attend the Fisheries History Section business meeting that will be held in conjunction with the Monterey meeting. Don't be scared off by the rather boring term "business meeting." Our annual meeting of Section members is painless, and it is our one opportunity each year to discuss fisheries history and current and future activities of the section.

The Section business meeting will be held on:

SUNDAY, AUGUST 24th
from 3:00 to 5:00 PM
in the San Carlos I room,
which is in the Marriott Hotel

The two conference hotels, the Marriott and the Doubletree, are connected to the Monterey Convention Center, and all business meetings, hospitality suites, technical sessions, trade show exhibits, etc. will be in one of those three locations.

I plan on moving quickly through most of the items on the agenda so that we can concentrate on two subjects: the future of the Fisheries calendar that the Section has been selling for several years, and membership, which has been level for several years. I plan to leave plenty of time so that members can discuss those two topics (in particular) and bring forth their ideas and suggestions. I encourage all of you to attend and participate. Please mark *August 24th, from 3:00-5:00 PM* on your calendars.

ASIH MEETING

Mark Jennings and Kurt Dunbar are to be congratulated on organizing a very informative and successful special session on, "Four Decades of Research Excellence: the Scientists, Personnel, Equipment, and Natural History Collections of the U.S. Fish Commission Steamer *Albatross* (1882-1921)," that was presented at the Annual Meeting of the American Society of Ichthyologists and Herpetologists in Seattle on July 1st. If you enjoy history, particularly that involving natural history, you would have enjoyed the daylong session that was co-sponsored by the Fisheries History Section. The room was usually packed all day long as 11 speakers discussed the scientists, the cruises, and the implications of the collections made by the *Albatross* and its crew. If you were unable to attend, be looking for the papers to appear in a future issue of *Marine Fisheries Review*. Editor Willis Hobart is working with Mark and Kurt to publish the papers in a special issue of *MFR*.

SOUTHERN CALIFORNIA FISHERIES

Ed Henke, who has been conducting research on fisheries history for many years, has asked Section members for assistance. Ed is particularly interested in two subjects:

(1) Does anyone have any information on August Ulrich, a German immigrant who joined a Geodetic Survey Group and traveled from San Diego to the Columbia River? Does anyone know of the existence of diaries, journals, or records of his travels? He traveled north through California prior to 1876, and Ed is particularly interested in any references to rivers, creeks, species of fish, etc. because of his principal area of interest (see No. 2) .

(2) A native of southern California, Ed Henke has long been investigating early records of distribution and abundance of migratory fishes in southern California, particularly steelhead. He is interested in any records from San Luis Obispo, Santa Barbara, Ventura, Los Angeles, Orange, San Bernardino, Riverside, or San Diego counties as well as Baja California. In particular, he is interested in any historical material for Huasna, Alamo, Santa Maria/Cuyama, Santa Ynez, Ventura, Santa Clara, and Malibu rivers and creeks. Many of these once contained steelhead.

Ed is always on the lookout for, not only written accounts, but the recollections of people born in southern California prior to 1920 who may be able to provide oral accounts, newspaper clippings, postcards, periodicals, diaries, etc. If anyone can help Ed, or pass along source suggestions or names, addresses, or telephone numbers of people who might have personal recollections, you can contact him at:

Ed Henke
Historical Research

769 Lisa Lane
Ashland, Oregon 97520
Telephone: 541-482-9578

REVIEWERS FOR FISHERIES

Kristen Merriman-Clarke, Editor of *Fisheries*, has asked that we spread the word to members that *Fisheries* is on the lookout for reviewers of scientific articles as well as book reviewers. Kristen would like to maintain a listing of potential reviewers, with their particular specialities and/or interests. If interested, you can contact her at 301-897-8616, extension 220, or e-mail her at kclarke@fisheries.org.

NOTES FROM AFS SUB-UNITS

Some fisheries history notes from Chapters, Divisions, and other Sections:

>>>The Atlantic International Chapter newsletter reports a new state record rainbow trout caught in New Hampshire. The 15 lb., 17.2 oz fish was captured by a fly fishing angler on the Pemigewasset River near Bristol, NH, on September 16, 1996. The fish was 35.5 inches long, with a girth of 18.25 inches, and beat the previous record, set in 1978, by almost 1.5 pounds.

>>>The Introduced Fish Section reports that "Nonindigenous Aquatic and Selected Terrestrial Species of Florida," an accounting of the status, pathway, time of introduction, present distribution, and significant ecological and economic effects of introduced plants and animals, has been published on the Internet (http//aquat. ifas.ufl.edu/National Biological Service. Publisher is the University of Florida, Center for Aquatic Plants......The Section also reports the presence of European green crabs in Oregon and the crayfish, *Orconectes rusticus*, now thriving in Wisconsin and Michigan.

>>>The oscar, a popular aquarium fish, was introduced into parts of Broward or Dade County, Florida, at least 25 years ago, and earlier elsewhere.. Recently, it has become a popular sport fish with anglers, with one survey reporting oscars accounted for 63% of fish captured.

Retrieving a beach seine to collect specimens for the 1928 publication, *Fishes of Chesapeake Bay* by Hildebrand and Schroeder.

THE ORIGINS OF BIG-GAME TUNA SPORT FISHING

Charles Holder is credited with catching the first large tuna--a 183 pound bluefin--with rod and reel in 1898. It had long been assumed that open water, migratory fishes, such as most tuna, were unavailable to most sports anglers. Holder's accomplishment, off Catalina Island, California, took almost four hours to achieve, and his boat capsized once during the struggle.

Holder soon formed the Catalina Tuna Club--obviously, he initially held the Club record. The Club had a number of rules, including the use of rod and reel only and a maximum of 72-lb test line. Within one month of the founding of the club, there were 24 members, each of whom having caught a tuna weighing in excess of 100 pounds. Soon, Club members were wearing special buttons, and wealthy anglers flocked to Catalina's waters from all over the world. Most were business tycoons, but one of the more famous early tuna anglers was writer Zane Grey.

*****Summarized from *Fishing: An Angler's Miscellany*, edited by Mark Hoff, Ariel Books, Kansas City, 1995.

RECENT FISHERIES HISTORY PUBLICATIONS

Casada, J. 1997. Dr. James Henshall: the father of American bass fishing. Bassmaster 30(7): 34-38.

Cone, J., and S. Ridlington. 1996. The Northwest salmon crisis: a documentary history. Oregon State University Press, Corvallis. 374p.

Cuvier, G. 1995. Historical portrait of the progress of ichthyology, from its origins to our own time, edited by T.W. Pietsch, translated by A.J. Simpson. Johns Hopkins University Press, Baltimore. 504p.

Dunn, J.R. 1996. Charles H. Gilbert, pioneer ichthyologist and fishery biologist. Marine Fisheries Review 58(1-2): 1-2.

Dunn, J.R. 1996. Charles Henry Gilbert (1859-1928) Naturalist-in-Charge, and Chauncey Thomas, Jr. (1850-1919), Commanding: conflict aboard the U.S. Fish Commission Steamer Albatross. Marine Fisheries Review 58(1-2): 3-16.

Dunn. J.R. 1996. Charles Henry Gilbert (1859-1928) naturalist-in-Charge: the 1906 North Pacific Expedition of the Steamer Albatross. Marine Fisheries Review 58(1-2): 17-28.

Franke, M.A. 1996. A grand experiment [the first half century of fisheries research and management in Yellowstone National Park]. Yellowstone Science 4(4): 2-7.

Mighetto, L., and W.J. Ebel. 1994. Saving the salmon: a history of the U.S. Army Corps of Engineers' efforts to protect anadromous fish on the Columbia and Snake rivers. Historical Research Associates, Inc., Seattle. 262p.

Peterson, K.C. 1995. River of life, channel of death: fish and dams on the lower Snake. Lewis-Clark State College, Lewiston. 321p.

Steimle, f.W., J.M. Burnett, and A.B. Theroux. 1995. A history of benthic research in the NMFS Northeast Fisheries Science Center. Marine Fisheries Review 57(2): 1-13.

SOME PUBLICATION NOTES

The paper, "Tragic remedies: a century of failed fishery policy on California's Sacramento River, " by Michael Black, won the Louis Knott Koontz Memorial Award for the best paper appearing in *Pacific Historical Review* in 1996..........Check out the interesting article on Dr. James Henshall, President of the AFS from 1891 to 1892, in the July/August issue of *Bassmaster*. Among other career highlights, Henshall was President of the Ohio Fish Commission, Secretary of the Cincinnati Society of Natural History, and superintendent of several U.S. Fish Commission hatcheries. He wrote the classic book, *Book of the Black Bass*, and prepared an exhibit on bass for the 1893 Columbian World's fair in 1893. He is known by many as the "Father of Bass Fishing." Thanks to Paul Brouha for sending a copy of the magazine.

CHANGES IN THE FISH COMMUNITY OF LAKE ONTARIO

Stan Smith kindly provided a copy of a relatively recent report by the Great Lakes Fishery Commission. Their Technical Report 60, "*Early Changes in the Fish Community of Lake Ontario*," was written by Stan over 20 years ago before he retired. This 38-page publication provides interesting historical background about the many changes that have occurred in the lake, and we have included the Abstract below, as printed in the report:

"Lake Ontario may have had the highest fishery yields of any of the other deepwater Great Lakes, but these catches occurred before the mid-1800s--before catches were recorded. The Atlantic salmon (*Salmo salar*) was the most-valuable species in the early fishery and was severely depleted before a quantitative account of the fishery could be made. Drainage modifications also contributed to the extinction of salmon in Lake Ontario; by 1845, a total of 7,406 water-powered sawmills were being operated in the state of New York. Forest removal further degraded spawning and nursery streams and affected recruitment of obligate and facultative stream spawners. The alewife (*Alosa pseudoharengus*) probably invaded Lake Ontario from the Erie Canal. By the late 1800s, the alewife was associated with declines of planktivores and piscivores, a pattern that occurred in the upper lakes in the mid-1900s. A close examination of early accounts of the sea lamprey (*Petromyzon marinus*) in the Lake Ontario watershed shows that the first reliable sighting was in 1835. Misidentification of the sea lamprey resulted in reports that it was endemic to the lake. Sea lampreys probably gained access to the lake from the Erie Canal, but because of degraded stream conditions, they did not become abundant in Lake Ontario until after the early 1900s when lake trout (*Salvelinus* *namaycush*) stocks collapsed."

Thanks, Stan, for providing a copy. Interested readers can obtain a reprint from the Great Lakes Fishery Commission, 2100 Commonwealth Boulevard, Suite 209, Ann Arbor, Michigan 48105-1563.

THE ORIGINS OF THE MARINE AQUARIUM

Whoever the first person was who tried to keep marine animals in an aquarium was probably the first person to realize that seawater soon becomes "stagnant," and the animals die and stink up the house. This idea of stationary water, gradually losing oxygen, was proposed at least as far back as 1721 by Richard Bradley. His suggestion: to make small ponds at the shoreline with water that could be replenished by the actions of the tides. He suggested an interesting two-wheel apparatus to expedite the action. Alternatively, he suggested a way of artificially salting trapped water.

The one sure way of keeping marine animals alive was to replenish the water (entirely) every day. This, of course, was very labor intense and required the aquarium enthusiast to devote much of his or her life to the hobby. Goldfish were commonly maintained just this way in freshwater in the early 1700s. Sir John Dalyell was wealthy enough to arrange for fresh sea water to be brought to his home aquarium every day. He managed to keep a sea anemone alive for 28 years and other animals alive for lesser periods of time.

The next step was to include living plants in aquaria. That helped, though most people were unaware why, even when an Edinburgh naturalist, Patrick Neill, noticed that a pet fish was quite lively when swimming near plants compared to other parts of the aquarium.

An English surgeon, Nathaniel Bagshaw Ward, is considered the "Father" of the modern aquarium. In 1830, he used some glass-sided containers of the type developed by a Scottish horticulturist in 1825 to maintain large numbers of plants. They survived and flourished, and he wrote an account of his observations, ***On the Growth of Plants in Closely-Glazed Cases*** that was published in 1842. Later, of course, similar containers were used to maintain aquatic animals.

*****Summarized from a small portion of ***The Naturalist in Britain: A Social History*** by David Elliston Allen, Princeton University Press, Princeton, NJ, 1976.

MUSEUMS OF THE FUTURE (FROM A LECTURE DELIVERED BY GEORGE BROWN GOODE TO THE BROOKLYN INSTITUTE, FEBRUARY 28, 1889)

"I hope and firmly believe that every American community with inhabitants to the number of five thousand or more will within the next half century have a public library, under the management of a trained librarian. Be it ever so small, its influence upon the people would be of untold value. One of the saddest things in this life is to realize that in the death of the older members of the community so much that is precious in the way of knowledge and experience is lost to the world. It is through the agency of books that mankind benefits by the toil of past generations and is able to avoid their errors."

"The people's museum should be much more than a house full of specimens in glass cases. It should be a house full of ideas, arranged with the strictest attention to system.....Like the library, it should be under the constant supervision of one or more men well informed, scholarly, and withal practical, and fitted by tastes and training to aid in the educational work."

"I should not organize the museum primarily for the use of the people in their larval or school-going stage of existence. The public-school teacher, with the illustrated text-book, diagrams, and other appliances, is in these days a professional outfit which is usually quite sufficient to enable him to teach his pupils. School days last, at the most, only from five to fifteen years, and they end with the majority of mankind before their minds have reached the age of growth most favorable for the reception and assimilation of the best and most useful thought. Why should we be crammed in the times of infancy and kept in a state of mental starvation during the period which follows, from maturity to old age, a state which is disheartening and unnatural, all the more because of the intellectual tastes which have been stimulated and partially formed by school life."

A drawing of a California sea lion made during the Hernando de Grijalva expedition along the California coast in 1533

THE ORIGINS OF HATCHERY RAINBOW TROUT

Bob Behnke, of Colorado State University is certainly the authority on historical aspects of trout culture (and other salmonid subjects) and he has written numerous articles on the subject. The following is extracted from an interesting article, "Livingston Stone, J.B. Campbell, and the Origins of Hatchery Rainbow Trout," that was originally published in *The American Fly Fisher*, Fall 1990. Bob kindly passed along the full article for Fisheries History Section members.

"I was pleased to read the article on Livingston Stone, authored by Frank E. Raymond, in the Spring 1990 issue of *The American Fly Fisher*. I regard Livingston Stone as a role model for the fisheries profession....."

"The historical information given in Mr. Raymond's article on Livingston Stone, J.B. Campbell [John Blizzard Campbell: editor], and the early propagation of rainbow trout from the McCloud River reflects three major points of error that have been thoroughly incorporated into angling and fisheries literature during the past 100 years. I believe *The American Fly Fisher* is an appropriate publication to document the corrections of these errors.

1. The first rainbow trout propagated in fish hatcheries did not come from the McCloud River, but from waters of the San Francisco Bay area, propagated by the California Acclimatization Society starting in 1870.

2. The first hatching of eggs of McCloud River rainbow trout was in 1877 by J.B. Campbell and Myron Green (an assistant to Livingston Stone) on "Campbell Creek" on Campbell's ranch. The propagation of McCloud River rainbow trout by the U.S. Fish Commission began in 1880, under the supervision of Myron Green on Crook's Creek (later, Green's Creek).

3. The rainbow trout propagated from the McCloud River was a mixture of steelhead and a nonanadromous fine-scaled trout ("red-banded trout of Livingston Stone). There never was a pure "Shasta" rainbow" in fish hatcheries: it was a hybrid mixture from the start.

Thus, the common belief that all hatchery rainbow trout trace their origins to the McCloud River is erroneous. It is also erroneous that "pure" McCloud or "Shasta" rainbows presently occur in Argentina or elsewhere as a result of early stocking (an article in the August, 1990 issue of the *Orvis News* tells of catching a "turbo-charged McCloud rainbow" in Argentina). Besides the few hundred thousand eggs taken and sold by Campbell and Green during 1877-1879, the propagation of McCloud River rainbow trout by the U.S. Fish Commission lasted from 1880 through 1888. During these nine years, only 2,676,725 eggs were shipped. From about 1890 to 1900, the U.S. Fish Commission found new, much more abundant sources of rainbow trout eggs to ship to federal, state, and private hatcheries in steelhead runs from the Klamath, Willamette, and Rogue rivers, Oregon, and from Redwood Creek, California. It can be assumed that any hatchery stocks of McCloud River Trout were overwhelmed by this massive infusion of steelhead eggs (the first shipment of rainbow trout eggs to Argentina in 1904 consisted of "20,000 steelhead" and "50,000 irideus" (probably domesticated hatchery rainbows)."

QUOTES FROM HISTORY

On the value of appropriating money for the U.S. Geological Survey:

"About 1853 there was a law passed that abolished a geological survey which had been established by the United States Government. That survey had started out just as this one has, but it never got so far. The statesmen of that day saw at once how extravagant it was to become, and they promptly abolished it. We should do the country a service if we should abolish this."

Rep. Hilary Herbert, *Congressional Record*, May 18, 1892

On appropriating money for exploring and preservation of collections for the Smithsonian Institution:

"What do we care about stuffed snakes, alligators, and all such things?.... Here is an appropriation of $6,000 for a most worthless purpose, and what right have we to appropriate it?....I am tired of all this thing called science here.... We have spent millions in that sort of thing for the last few years, and it is time it should be stopped."

Sen. Simon Cameron, in a Senate Debate, February 21, 1861

Report on the value of the Grand Canyon and Colorado River region:

"The region last explored is, of course, altogether valueless. It can be approached only from the south, and after entering it there is nothing to do but leave. Ours has been the first, and will doubtless be the last, part of whites to visit this profitless locality. It seems intended by nature that the Colorado River, along the greater portion of its lonely and majestic way, shall be forever unvisited and undisturbed."

Report to Congress, 1861, by Lt. Joseph Ives, U.S. Army Corps of Topographical Engineers after visiting the region in 1857 and 1858

On funding the National Zoological Park:

"I do not believe the American people, hundreds and thousands of whom are to-day without homes, ought to be taxed to afford shelter and erect homes for snakes, raccoons, opossums, bears, and all the creeping and slimy things of the earth."

Rep. Snodgrass, *Congressional Record*, 1892

REMINDER: A CENTURY OF FISH CULTURE

The special day-long session, "A Century of Fish Culture," will be presented at two upcoming meetings. The session is co-sponsored by the Fisheries History and Fish Culture sections and will compare the state of culture knowledge 100 years ago, as described in the *Manual of Fish Culture*, with technology of today:

AFS Annual Meeting, Monterey, CA, August 26, 1997

Aquaculture '98, Las Vegas, NV, February 1998

JACQUES YVES COUSTEAU
(1910-1997)

"On a goggle dive at Djerba Island off Tunisia in 1939 I met sharks for the first time. They were magnificent gun-metal creatures, eight feet long, that swam in pairs behind their servant remoras. I was uneasy with fear, but I calmed somewhat when I saw the reaction of my diving companion, Simone. She was scared. The sharks passed on haughtily.

"The Djerba sharks were entered in a shark casebook I kept religiously until we went to the Red Sea in 1951, where sharks appeared in such numbers that my census lost value. From the data, covering over two hundred shark encounters with many varieties, I can offer two conclusions: the better acquainted we become with sharks, the less we know them, and one can never tell what is shark is going to do.

"Man is separated from the shark by an abyss of time. The fish still lives in the late Mesozoic, when the rocks were made: it has changed but little in perhaps three hundred million years. Across the gulf of ages, which evolved other marine creatures, the relentless, indestructible shark has come without need of evolution, the oldest killer, armed for the fray of existence in the beginning."

***The Silent World*, 1953**

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THE NATIONAL GEOGRAPHIC MAGAZINE

OUR HERITAGE OF THE FRESH WATERS

Biographies of the Most Widely Distributed of the Important Food and Game Fishes of the United States

By CHARLES HASKINS TOWNSEND

DIRECTOR OF THE NEW YORK AQUARIUM

With Sixteen Color Plates from Paintings by Hashime Murayama

SINCE the beginning of time mankind has been able to get some part of his food from the waters; among the relics of the Stone Age are shell hooks and stone sinkers. Ancient sculptures—Assyrian, Egyptian, and Aztec—portray the taking of fishes with spear, hook, and net.

The prophet Habakkuk—who knows how many centuries B. C.?—placed some details on fishing in the earliest literature: "They take up all of them with the angle, they catch them in their net, and gather them in their drag."

In some of the far corners of the world amazingly primitive ways of getting fishes are still in use.

In the mountain streams of New Guinea the still-savage native has been found using a dip net made of a hoop fitted with a piece of unbelievably tough spider web.

We have seen the Aleut drag up a heavy halibut with a huge hook of bent wood, the Fuegian make a successful throw with his bone-pointed spear, and the Tonga islander stupefy hundreds of fishes with the juices of a poisonous plant.

The modern Japanese fisher has not yet lost the ancient art of making the cormorant fish for him without the trouble of providing either hook or bait.

As populations increased and man improved his methods, he naturally took more food from the waters and doubtless wasted more; and this he is still doing. His equipment is now enormous and a surplus fish supply often gluts the market, despite cold storage and other means designed to prevent it.

As fish-catching enterprises gradually became great fishery industries, there arose the problems of diminishing supply. The sea fisheries stood the strain so well that some naturalists of the past generation took the stand that the puny efforts of man could not affect the life of the sea; but this view has undergone a change. To-day there are official boards in many countries concerned with the preservation of sea fisheries.

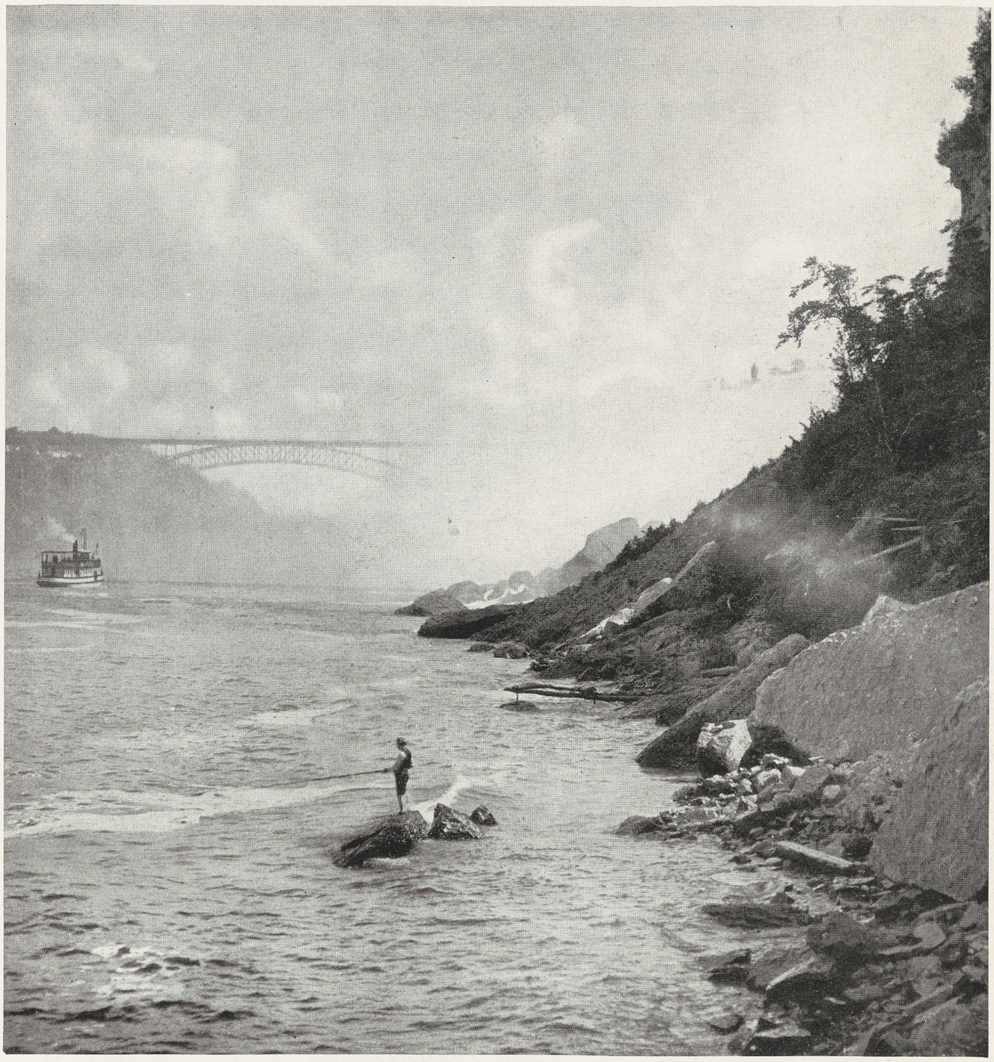
OUR FRESH-WATER FISH RESOURCES ARE CONSTANTLY DIMINISHING

In considering the resources of our fresh waters, we find everywhere exhaustive methods of fishing and a diminishing supply, in spite of restrictive measures and extensive fish propagation.

The means by which diminution is measured are to be found in the fishery statistics of the past half century. The annual yield of products—still very large—can be safely viewed only in com-

FISHING IN SKYKOMISH RIVER NEAR INDEX, WASHINGTON

There are several kinds of Trouts in the waters of Washington State, mostly the "Cutthroat" forms, which are more numerous in the Rocky Mountain region.



Photograph by Eugene J. Hall

FISHING BELOW NIAGARA FALLS

The Great Lakes constitute a vast inland reservoir of fish life, the annual commercial catch sometimes exceeding 100,000,000 pounds.

parison with the continual increase and improvement in the apparatus of capture.

It takes more and more gear to make the same catch. In the Great Lakes, our largest reservoirs of fish food, the investment in the fishery industry now exceeds $10,000,000. The principal fish-catching devices, such as pound nets, fyke nets, and gill nets, practically automatic in operation, are filling day and night as long as the Lakes are free from ice.

The rivers and lakes of the United States have fishery resources that are unequaled elsewhere. The Great Lakes are virtually inland seas and the navigable rivers are among the largest in the world. The mighty Mississippi, with its tributaries reaching in all directions, fairly dominates the map of the country.

These waters, with the rivers of the Atlantic and Pacific coasts and many lakes of the Northern States, have been enormously productive in food for our people.

In one year commercial fishermen alone have taken from the Mississippi River

Photograph by Scenic America Company

FISHING IN CRATER LAKE, CRATER LAKE NATIONAL PARK, OREGON

There were no fishes in Crater Lake until Rainbow Trout were introduced by the Government. Crater Lake is six miles long, four miles wide, and in one place 2,000 feet deep. Its surface is 6,000 feet above sea-level, its steep walls rise from 500 to 2,000 feet above its surface, and it has neither inlet nor outlet that has yet been discovered.

and its tributaries more than 96,000,000 pounds of fish, while the Great Lakes yielded more than 113,000,000 pounds.

Large as are the food supplies of these two regions at the present time, they must have been vastly greater before the exploitation of their resources began. Unfortunately, there are no official records by which the extent of the earlier fishery operations may be measured.

While the fish food derived from our fresh waters is vast in quantity, it is also notable in variety. There are many kinds of Trouts, Salmons, Whitefishes, Sturgeons, Pikes, Basses, Sunfishes, Perches, Catfishes, the Shad and the Eel, as well as the less important, but abundant and widely distributed, Chubs and Suckers.

SERIOUS INROADS BEING MADE ON SALMON AND SHAD

Although the Salmons, Sturgeons, the Shad and other fishes ascending rivers for the purpose of spawning do not remain permanently in the fresh waters, it is here only that they reproduce and may be captured. It is here that they will be preserved indefinitely or utterly destroyed.

None of the rivers of the Atlantic coast contain to-day the great runs of Shad, Sturgeon, and Salmon for which they were noted half a century ago. Along the Pacific coast from California to Alaska the Salmon rivers have been subjected for more than a generation to commercial fishing so exhaustive that the prepared products are distributed by the shipload throughout the civilized world.

In the larger Pacific rivers the migrating Salmons pass up to their spawning grounds more than a thousand miles inland only after the nets of the canneries have taken their heavy toll, amounting to the great bulk of the migrants. The fresh-water crops planted by nature are being gathered at a rate that tends to increase rather than diminish.

When restrictions are proposed by conservationists, the extent of the "investment" is at once pointed out and greater propagation is urged instead. It is difficult to check a going industry, even when it is clear that its future is being imperiled.

The average citizen sees but little of the great fishing operations going on perpetually. The innumerable gill nets, pound nets and fyke nets—all under water and out of sight—work while the fishermen are asleep. From early spring until late autumn they are emptied daily and the heavy catch distributed to the markets of the whole country. In winter the markets continue to supply great quantities of fish withdrawn from cold storage.

We think little about where our fish supplies come from so long as we have them, and Uncle Sam's statistics, even when recording the annual catch in such figures as hundreds of millions of pounds, are but dull reading. It is well to be reminded, however, that the yield of the fisheries grows smaller—not larger.

In addition to the familiar food and game fishes, our waters are rich in Minnows, Darters, Shiners, and other small fry of no direct economic value, but of vast importance as the food supply of larger fishes. Every great watershed has its peculiar forms of these, all well known to ichthyologists, who have described and named them by the score.

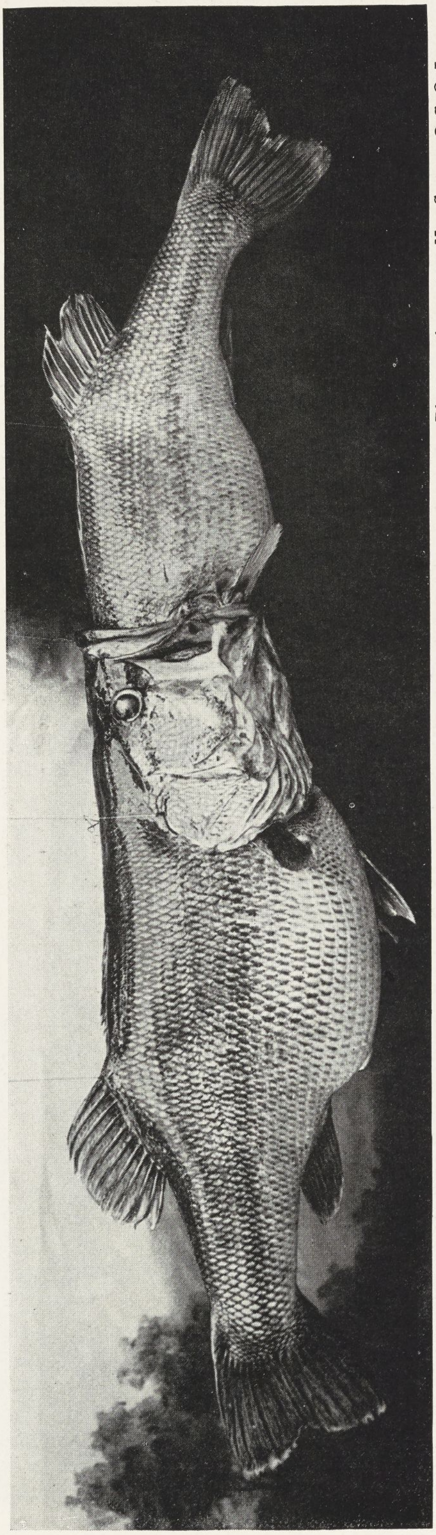
Some of our smallest fishes have been found useful in combating malaria and annoyance caused by mosquitoes, and are even being shipped by the United States Bureau of Fisheries to mosquito-plagued foreign countries. There is now in progress much active investigation regarding the value of several species of fishes for the control of the mosquito.

UNITED STATES HAS FIVE TIMES AS MANY KINDS OF FISHES AS EUROPE

The richness of fish life in our fresh waters is amazing. The United States has a smaller area than Europe, yet it has nearly five times as many kinds of fresh-water fishes. We have about 585 species of these, while Europe has but 126 species.

We find that a single State may have considerably more than 100, the number known to Illinois being 150, while New York is credited with 141. It could doubtless be shown that our fresh-water fishery resources are greater than those of any other country.

Many of the fishes commonly taken for food or in sport fishing, and naturally of wide distribution, have, as a result of fish-cultural operations, been established in sections of the country far removed from their original habitat.



Photograph courtesy Noa Spears, © C. O. Lee

A CANNIBAL BASS FALLS A VICTIM TO HIS APPETITE

These two fish were picked up by a boatman while they were still struggling in Medina Lake, near San Antonio, Texas. The large Bass had the entire head of the smaller Bass in his mouth. Hungry Bass sometimes try to swallow fishes larger than they can manage comfortably, even their own species. The cannibal shown above is the Large-mouthed Black Bass. Like the Pickerel, he can digest a particularly large mouthful by inches.

A fish belonging to the Mississippi system or to the Atlantic slope often takes full possession of a new watershed, as the result of mere transplantation of limited numbers. In this way the Shad and the Striped Bass have been made abundant on the Pacific coast—a notable success in fish propagation.

FISHING AS A LURE FOR THE TOURIST

Although the numbers of fishes caught by anglers do not figure in statistics of the catch made for market, they are not without high economic and other values. Most of the Northern States are visited in summer by tourists interested primarily in good angling waters.

Lakes far and wide have become summer resorts for people who find much of their recreation in fishing. Railways and summer resorts widely advertise the resources of their waters. Summer visitors, moving actually by hundreds of thousands, carry into these States millions of dollars. The trade in angling equipment alone is extensive.

Who can measure the health and esthetic values attendant upon the angling idea? Some one has recently asserted that the angling habit is conducive to long life, and, beginning with Izaak Walton, who lived to be ninety, presents a lengthy list of celebrated fishermen who lived well into the eighties and nineties, many of them prominent in the literature of American angling.

FISH PROPAGATION

Modern fish culture has made greater progress in the United States than in other countries, being carried on by the Federal Government and by all of the States which have fishery resources of importance. The output from Government hatcheries alone in 1921 amounted to nearly five billions of fish eggs, young fry, and partly reared fishes, while that from State hatcheries was nearly as great.

The work includes all of the fresh-water fishes of importance and a

Photograph by Redner Photo Company

THE CATCH OF ONE ARKANSAS FISHERMAN—118 FISH TAKEN IN TWO NIGHTS AND ONE DAY

All the larger specimens shown here are Catfishes. There is good fishing in the streams of Arkansas; they have contributed to the markets in a single year 500,000 pounds.

Photograph by S. N. Leek

A NATIVE SON AND NATIVE TROUT: WYOMING

The Trout shown here are doubtless one of the numerous species of the Rocky Mountain region, known as Black-spotted or "Cutthroat"—probably the Yellowstone Trout (*Salmo lewisi*) inhabiting the Snake River basin above Shoshone Falls.

number of marine species belonging to the coastal regions or entering the rivers to spawn. The hatcheries, both Federal and State, are distributed north and south from coast to coast.

POLLUTION OF FRESH WATERS A DANGEROUS MENACE TO OUR FISH RESOURCES

Fresh-water fish culture in the United States has been carried on for more than fifty years in steadily increasing volume, in the effort to keep pace with a depletion by fishery industries that constantly threaten exhaustion of the fish supply.

The great fishery problem of the time in our country is the pollution of the fresh waters by innumerable agencies, rapidly affecting their productiveness. Unless stern measures are introduced by law to correct this, soon one of our great natural economic gifts will be seriously stricken.

When we consider that the market catch in the Great Lakes alone sometimes exceeds 100,000,000 pounds a year, that legions of anglers are overfishing the Trout and Bass streams everywhere, and that pollution of the rivers by manufacturing industries has reached appalling proportions, it is apparent that our heritage of the waters is endangered to a serious degree.

Fish culture alone cannot save it, even if greatly increased. We are already wasting expensive propagation work in stocking waters no longer suitable for fish life, and many streams have been abandoned to their fate. One could name a score of rivers in mining and manufacturing States, once contributing to the food supply, that now contain no living thing—no fish or Mussel or Crayfish, not even the air-breathing Frog. These rivers represent damaged resources and there are others that may soon be like them.

Reforms come so slowly that the great cleaning-up task ahead of the American people is not likely to be undertaken seriously until conditions become intolerable. In many countries all wastes available for fertilization are restored to the land and not sent insensately through sewers into the streams, while manufacturing wastes

Photograph by Harry F. Blanchard

HIS TRIBUTE OF THE DAY'S CATCH

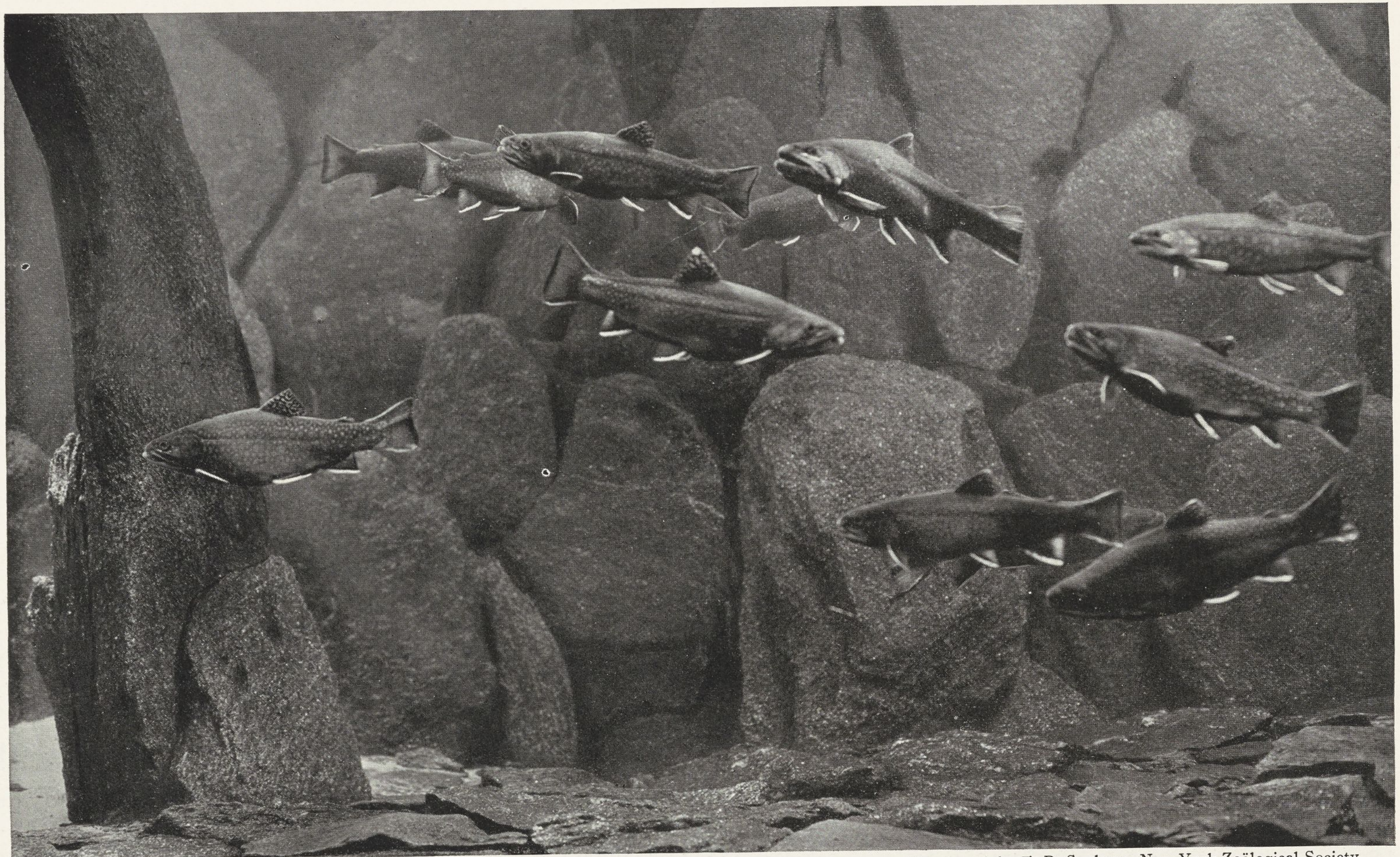
are converted into valuable by-products. The exhaustion of our fresh-water resources through overfishing and water pollution is not inevitable. There is now a saving fund of knowledge relative both to propagation and protective measures, awaiting application through the force of aroused and insistent public demand.

THE AUTOMOBILE AFFECTS FISH SUPPLY

A more recent but increasing danger to which angling waters are exposed lies in the ever-increasing use of the automobile. Bass and Trout waters heretofore reached with difficulty have become the easily accessible resorts of camping parties, with the result that their resources are being exhausted.

As a partial offset to such conditions, we may point to the increasing efforts of the United States Bureau of Fisheries in the work of rescuing food and game fishes from overflowed lands in the Mississippi Valley, where appalling numbers of fishes have always perished upon the recedence of floods.

Although a dozen or more crews of five or six men each, equipped with seines, are now employed, many times the present number are needed. The total number



Photograph by E. R. Sanborn, New York Zoölogical Society

THE INCOMPARABLE BROOK TROUT, BEST BELOVED BY THE LIGHT-ROD FLY-FISHER

This fish thrives in cold torrents which grosser fishes do not enter. No part of our outdoor heritage is more worthy of conservation than the rapid Trout waters of the mountains.

of entrapped fishes restored to flowing waters in 1922 exceeded 179,000,000 of all sizes. The larger fishes are removed to adjacent streams, the smaller ones distributed far and wide for the stocking of depleted waters.

Many as are the sportsmen taking toll of our wild life with the gun, those who use the rod are vastly more numerous. It is as easy to exhaust a small stream by overfishing as it is to exhaust the quail supply of a neighborhood. Fortunately, the preservation of the fishes is always possible through the employment of safeguards and restorative measures. Our fishing will doubtless last longer than our shooting.

Private fish culture would be of great service in maintaining and increasing our supply of fish food. While it has been practiced for centuries in some European countries, it has but little more than commenced in America.

The possessors of strongly flowing springs, brooks, and small lakes should be awakened to the value of their home resources for water farming. Approved methods for the construction and management of fish ponds have been worked out at public fish-cultural stations and instructive public documents on the subject can be had for the asking.

Fish-culturists assert that an acre of water can be made to yield more food than an acre of land and the truth of the assertion has been demonstrated.

MUSSELS DEPENDENT UPON FISH HOSTS

An interesting work in aquiculture is now being carried on in the Mississippi Valley under the direction of the Bureau of Fisheries. It is based upon the fact that the propagation of the Mussel is dependent upon the presence of fishes to which the young, free-swimming Mussels may attach themselves as parasites until they are old enough to form shells and begin an independent existence.

The large, heavy-shelled Mussels of this region have been gathered in such numbers for the manufacture of pearl buttons, and also for the valuable pearls they sometimes contain, that the supply is being exhausted and the important industry dependent upon the Mussel is in danger.

The Mussel industry annually yields 60,000 tons of shells which are worth more than $1,000,000. We are all wearing pearl buttons from this source, which will be missed if the great river becomes too foul for the growth of Mussels.

Young Mussels attach chiefly to the gills of fishes, and in some species to the fins, during the early period of their lives. It is now practically certain that all Mussel spawn which fails to find a suitable fish host sinks to the bottom and dies.

The young Mussels are temporarily provided with minute hooks for attachment and are soon enveloped in the epithelium of the fish, where they remain encysted until the shell begins to form and they can safely drop off.

All fishes are not equally susceptible to these temporary mollusk parasites; some receive very few, others shed them too soon, while still others die as a result of carrying too many. Practical work is in progress, and large numbers of fishes "infected," as it is called, with young Mussels are liberated to stock the public waters, as their "parasites" develop and fall off.

The "planting" of the Mussels is, therefore, left to the fishes. It is even possible to send Mussel-bearing fishes to waters outside the Mississippi system and thus introduce the more valuable Mussels elsewhere.

TURTLES, FROGS, AND CRAYFISH

There are several species of large Turtles of the kinds known as "sliders" in our fresh-water streams and lakes, especially in the Middle and Southern States, that contribute to the food supply. They have long been used in filling the ever-widening vacancy in the markets formerly occupied by that favorite of the epicure, the Diamond-backed Terrapin of the salt-water marshes.

They have so high an edible value that it is whispered we often pay Terrapin prices for Turtles that never saw brackish water. Fishery officials are aware of their importance and have studied their distribution, methods of capture, and conservation.

Frogs of several kinds are valued aquatic food delicacies, and their habits have received considerable attention with the view to developing a practical system of frog-culture. It is to be hoped that some method of conservation will be

Photograph by Fred H. Kiser

AMONG THE CHALETS OF THE CUTBANK VALLEY, GLACIER NATIONAL PARK: MONTANA

The United States Government established a fish hatchery in Glacier National Park recently and has planted nearly 4,000,000 fish there in the last two years. The waters of the park abound in Rainbow, Brook, and Mackinaw Trout, Grayling, and Whitefish.

Photograph by Putnam Studios

TROLLING FOR TROUT IN LAKE TAHOE

The Lake Tahoe Trout (*Salmo henshawi*) inhabits several lakes of the high Sierra. It attains a weight of six pounds. There is also a Deep-water Trout in this lake (*Salmo tahoensis*), which is never found in shallow water.

Photograph by William H. Zerbe

ON HIS WAY TO THE HUNTING GROUND OF YOUTH

Photograph by Maynard Owen Williams

FISHING IN THE POTOMAC FROM THE NATIONAL CAPITAL'S WATERFRONT

found before the natural supply approaches the point of exhaustion.

The annual market supply of fresh-water Turtles and Frogs has been known to exceed half a million pounds of each, the great bulk of the catch being derived from the Mississippi and its tributaries.

The humble Crayfish, although of small size, figures prominently in the aquatic food supply, Lake Michigan leading with over 200,000 pounds annually.

FOODS OF FISHES

A subject of perpetual interest to all who fish with the rod is the food of fishes. There are moments in the lives of all of us when the most important thing in the world seems to be how to get the fish to bite. The problem is taken as seriously by the captain of some great industry, off on a fishing trip, supplied with the most expensive tackle, as by the barefooted urchin with a homemade pole, and doubtless the man of business is the more serious of the two.

Thanks to the patient laboratory investigations of Professor S. A. Forbes, this dark question has been made luminous. He tells us that while the food of fishes consists chiefly of other fishes, it includes practically the whole aquatic fauna—a comforting fact when we would seek for baits.

Fishes not only feed on other fishes and on insects, but on crustaceans, mollusks, and worms. Plants do not constitute much of their food, although a few kinds feed on them, such as Buffalo-fishes, Carps, and Minnows. Some fishes get food by rooting in mud, while others are inclined to be scavengers.

Among the chiefly fish-eating fishes may be mentioned Pike, Pickerel, Muskellunge, Pike-perch, Burbot, Gar, Black Bass, and Channel Catfishes. Those taking fish food in moderate amounts are represented by Bream, Blue-cheeked Sunfish, Mud-fish, White Bass, Rock Bass, and Crappie.

Fishes which feed on other fishes to a trivial extent are White Perch, Suckers, Spoonbill, the various Darters, Top Minnows and Silversides, Sticklebacks, Mud Minnows, Stone-cats, and common Minnows. The whole Minnow tribe contributes to the food of the smaller fish-eaters.

In the Mississippi region the Gizzard-shad constitutes 40 per cent of the food of the Wall-eyed Pike, 30 per cent that of

Photograph from U. S. Forest Service

LAKE TROUT CAUGHT IN SUPERIOR NATIONAL FOREST: MINNESOTA

The Great Lakes Trout, or Mackinaw Trout (*Cristivomer namaycush*), inhabits many of the larger northern bodies of water outside the Great Lakes. It is a good game fish, wherever found.

the Black Bass, half that of the Pike, and a third that of the Gars. This is a good illustration of the usefulness of an abundant species of little importance as food for man.

Mollusks—the Snails and Mussels of various species—are also important as fish food. They form large proportions of the food of Catfishes, Suckers, Fresh-water Drum, and Mudfish. About 16 per cent of the food of Perches, Sunfishes, Top Minnows, and Shiners is molluscan in character.

Fishes feed freely on insects, not only on the aquatic forms in their various larval and mature stages, but also on terrestrial insects cast into the water in many ways.

Crustaceans appear to be of even more importance as fish food, especially the minute Entomostraca. The Crayfishes are also eaten.

The food of adult fishes naturally differs greatly from that of the young. In addition to natural foods, both alive and dead, fishes in captivity will devour many kinds of meats and prepared foods. The question, then, as to what constitutes the food of fishes may be answered: almost any living animal forms from the water not too large to be swallowed. Therefore if the fish will not take the bait or the fly first offered, it may be tempted with another, and the resourceful angler need not return with an empty creel.

AGE, GROWTH, AND HABITS OF FISHES

Little can be learned definitely about the ages attained by fishes, unless individuals are kept under observation in captivity, either in public aquariums or in the ponds of fish-culturists.

The tagging experiments made on young fishes at Government Salmon hatcheries on the Pacific coast have yielded information as to the ages when these fishes, after attaining maturity in the sea, return to spawn in their native rivers.

As all of the five species of Pacific Salmons perish after their first and only spawning, tagging reveals only the age at breeding maturity, which seems to vary

© Haynes, St. Paul

CATCHING YOUR FISH AND COOKING IT WITHOUT MOVING FROM YOUR TRACKS

The Yellowstone Trout (*Salmo lewisi*) is very abundant in Yellowstone Lake, Yellowstone National Park. The "boiling pot" is one of the numerous hot-water holes to be found in this region. The surrounding water is cold.

between the fourth and the seventh year, according to the species.

The records of public and private aquariums, however, furnish data that we may consider reliable. The European Eel has undoubtedly lived for long periods in captivity. According to accepted authorities, a few specimens kept in aquariums have lived for periods varying from 20 to 55 years. Boulenger, in the Cambridge Natural History, states that an Eel kept by the French naturalist Desmarest for "upwards of 40 years" reached a length of four and a half feet.

It is recorded that four Russian Sterlets had lived in the private aquarium of Captain Vipan in Northamptonshire for 25 years. He also had a Golden Orfe still living after 24 years of captivity. A record from the Brighton Aquarium is that of a Sterlet which died after having been kept there "about 38 years."

The Australian Lung-fish is known to have lived at the London Zoölogical Gardens more than 19 years.

There are accounts of European Trout said to have been kept in captivity for 53 years, and of Carp still longer, but such are hardly comparable in verity with the records of existing public and private aquariums.

The New York Aquarium still has specimens (1923) of the Mudfish or Bowfin and the Long-nosed Gar which were received in 1903. There are also living Short-nosed Gars brought from the Mississippi River in 1904.

In the Aquarium certain North American fishes have lived for long periods, viz., Striped Bass, 20 years; Whitefish hatched in the building in 1913 are still living; Large-mouthed Black Bass, 11 years; Muskellunge, Calico Bass, Rock Bass, and Yellow Perch, 10 years. The last four were adults when received and are still living.

A Striped Bass kept in captivity for 19 years weighed 20 pounds and was three feet long when it died. Its length when received was about six inches. This species sometimes attains a weight of 80 pounds or more. It is likely that some

THE "FISHING ROD" OF THE OJIBWAY INDIANS OF NORTHERN MINNESOTA

Most of the northern tribes of Indians are adepts with the fish spear.

species grow faster in freedom, where they find their natural foods, but other kinds may develop faster in suitable ponds, where they are well cared for and protected from enemies.

Wild fishes of exceptionally large size being often found, we may assume that fishes continue to grow through life, the period of life depending largely upon enemies. In a world beset with sharp fangs and claws, the life of a wild animal, either in the water or on land, is apt to end in a tragedy.

TELLING THE AGE OF A FISH BY ITS SCALES

It is now known that the scales of fishes bear marks which indicate the length of life and the rate of growth in different years. Studies of the Atlantic Salmon in Scotland and of the various species of Pacific Salmon have proved this.

Photograph by T. J. Golden

A LAKE CHAUTAUQUA MUSKELLUNGE

This specimen, which was 52½ inches long, with a girth of 24½ inches, weighed 42 pounds (see text, page 157).

The scale grows in proportion with the rest of the fish, principally by additions around its border. The fish grows at different rates during different seasons of the year. Concentric ridges form around the edge of the scale, its marginal expansion in summer being more rapid than in winter, so that the growth during each year is usually distinguishable. (See illustration, page 153).

Studies of the five species of Pacific Salmons have shown the ages at which the different species return to the rivers to spawn. Thus, the ridges on a fish's scales are comparable to the annual ring growths revealed on a cross-section of a tree trunk, which tell its age.

It is interesting to note that the "tagging" of young Pacific Salmons, previously referred to, has already served to indicate that, after attaining maturity in the sea, each returns to spawn in the identical stream in which its life began.

Studies of the scales of Whitefishes in the Great Lakes have shown that the scale characters are so well defined that they indicate the age of the individual fish and the rate of growth of the species.

Scales from Whitefishes hatched and reared in the New York Aquarium and therefore of known age (see illustration, page 131) have been used by Government biologists in checking the results of studies of the scales of wild fishes.

The sexes of fishes are not as readily

Photograph by E. R. Sanborn

YOUNG SMALL-MOUTHED BLACK BASS WINTERING IN AN AQUARIUM

The fish remain poised in mid-tank, crowded closely together. As long as plants can be kept growing in the cold water the fish will pack themselves tightly among them. While the temperature of the water remains low, the fish seldom take food.

distinguishable as in the case of birds. Males and females are usually so much alike that only the expert recognizes the differences, and in many species the dissecting knife must be employed to determine the fact.

The colors of fishes vary somewhat according to the waters which they inhabit, and this applies also to fishes held in captivity, where their colors tend to become more subdued. The fishes of exhibition tanks, however, brighten their colors during the spawning seasons, much as do wild fishes.

The habits of fishes have not been studied as thoroughly as have those of birds, mammals, and other vertebrated animals. Books on fishes are largely of two classes: those written by anglers, relating chiefly to methods employed in the capture of the fish, and those written by the systematic naturalist, dealing chiefly with classification and distribution.

In neither class of books is the life of

Photograph by E. R. Sanborn

THE AMATEUR FISHERMAN'S DELIGHT: ROCK BASS

Whatever it may lack in reputation among scientific fishers, this species is one of the most popular among average anglers. From the St. Lawrence to Texas, the legion of the unskilled easily transfer it from its rocky haunts to the frying-pan.

the fish in its own environment very fully considered. There are, of course, satisfactory life histories of certain common species, especially those inhabiting the smaller streams, and fish-culturists are contributing new information on the ways of fishes reared in ponds.

Since the keeping of fishes in aquariums became common, many important facts have been recorded, but observations on creatures in captivity can manifestly deal with but little of their real life.

For many important facts relating to the senses of fishes we are indebted to the modern biological laboratory. Facts based on scientific experiment relative to fishes' powers of hearing and memory, their color changes, sleep, electrical and poisonous properties, the sounds they make, and so on, are slowly being brought to light.

The naturalist who can devote himself to the observation of the ways of fishes will find a fascinating field and contribute new facts to science.

SPOTTED CATFISH (Ictalurus punctatus), COMMON BULLHEAD (Ameiurus nebulosus) and other Catfishes

(*For illustration see Color Plate I*)

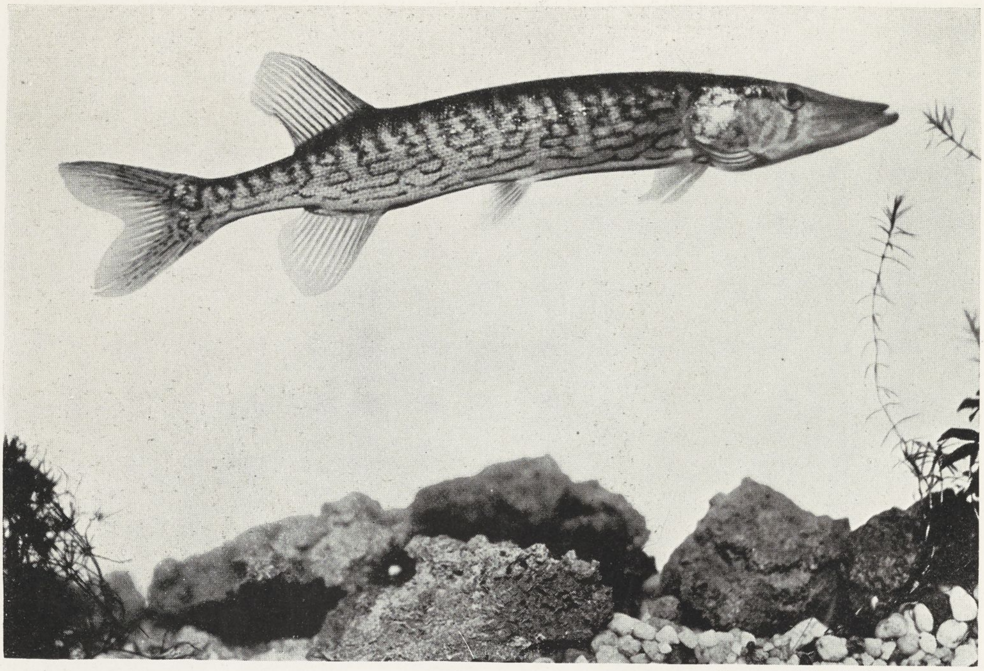
There are many kinds of Catfishes in the United States, all of which belong naturally to that part of the country lying to the east of the Rocky Mountains, those now abundant in some States west of the Rockies having been introduced.

Catfishes are of considerable importance commercially. The fishery statistics of a few years ago show that the annual catch for market exceeded 14,000,000 pounds, but to-day the supply is much smaller.

Being easy to catch, the total of those taken everywhere with hook and line can only be conjectured, but it may possibly equal the quantity yielded by the net fisheries.

As Catfishes in general have the habit of guarding their nests and protecting the young, the supply holds out well in spite of exhaustive fishing. Such habits also as feeding chiefly at night and feeding but little in winter contribute to their preservation.

The Blue Catfish, inhabiting the Mississippi Valley, is the largest and best of all as a food-



Photograph by E. R. Sanborn

THE EASTERN PICKEREL IS WIDELY DISTRIBUTED

This species inhabits every State east of the Alleghenies, where there are lakes, ponds, and slow streams. Bass and Trout fishers do not praise it, but thousands of others take it thankfully.

fish. It occasionally attains a weight of 125 pounds and 80-pound specimens are not uncommon, but like other fishes taken in large numbers, the average weight is only a few pounds.

The Blue Catfish is less inclined to live in muddy waters than some other species, preferring the clearer and swifter streams. It is a clean feeder, living much on fishes and Crayfish. As a game fish it is one of the best in the Catfish family, taking many kinds of baits, and is a strong fighter on the line, but never adds to the angler's thrill by leaping from the water.

The Blue Catfish is decidedly given to migratory movements according to seasonal changes in temperature, gathering in the more southerly parts of its range in winter.

The Spotted Catfish (*Ictalurus punctatus*) belongs in the Mississippi Valley and the Great Lakes. It does not reach the size of the Blue Cat, seldom weighing as much as 25 pounds. Like the Blue Catfish, it is a trim and active fish. There are four species in this genus, all having forked tails.

One of the best-known Catfishes is the Common Bullhead (*Ameiurus nebulosus*) inhabiting streams, lakes and ponds of the Eastern and Middle States and distributed as far westward as the Dakotas and Texas. Another fish of this round-tailed genus is the Black Bullhead (*Ameiurus melas*), having much the same distribution. The Bullheads are easily raised in ponds, and under proper management yield a good supply of white and palatable fish food. All of our native Catfishes have tough, scaleless skins and small eyes, and all have eight barbels or feelers on upper and under sides of the mouth, which are useful in searching for food in the muddy waters that many of them inhabit.

Catfishes make their nests usually in sheltered spots, such as can be found under rocks, submerged logs, and stumps, and do considerable excavating in enlarging them. They are springtime spawners. The eggs hatch in a few days and the young stay with the parent fish until about an inch long.

Catfishes in general are omnivorous, feeding on animal life, and are not averse to downright scavenging. They are very hardy and few fishes can live longer out of water. As they have dangerous spines on dorsal and pectoral fins, fishermen soon learn to handle them circumspectly.

As kept in tanks, Catfishes become nearly dormant when the water turns cold. A 60-pound Mississippi Catfish (*Leptops olivaris*), which lived in captivity several years, took no food during the winter months and remained practically motionless.

The name Channel Catfish is a term rather loosely applied by fishermen to several of the larger fishes of large streams.

Fully a dozen of our numerous kinds of Catfishes are important as food.

Photograph by E. R. Sanborn

TEN-YEAR-OLD WHITEFISHES

These specimens were hatched in the New York Aquarium. Being the only Whitefishes of known age available, scales from them are used by biologists in checking the results of studies of the ages of wild Whitefishes (see text, page 127).

THE BLACK BASSES (Micropterus dolomieu and Micropterus salmoides)

(*For illustration see Color Plate II*)

The two closely related Black Basses are easily distinguished by the size of the mouth and by the color pattern. In the Small-mouthed species the upper jaw does not extend beyond the eye, as in the case of the Large-mouthed Bass; in the former there is much dark blotching, which tends to form short vertical cross-bands, while the latter has usually a dark band along the side.

The expert angler thinks he can distinguish the species he has hooked before seeing it, as the Small-mouthed Black Bass is by far the gamier and more active. Its reputation as a game fish is not surpassed by any other of its size.

Although the Black Basses are cultivated and distributed both officially and by private effort, they are not fishes whose mature eggs can be stripped by hand and developed in hatchery buildings by wholesale methods. Their propagation is effected by the more natural but slower method of pond culture, in which the fishes are provided with the conditions most favorable to their mating and the rearing of their young.

The same limitations in culture apply to all fishes of the Bass-Sunfish family, which have the habit of making nests and protecting their young.

The Small-mouthed Bass is the fish that pond-owners find most satisfactory and they are justified in the selection. Much of its present wide distribution is due to this fact.

This truly American fish has been much written about and naturally has many names in its extensive range, but Small-mouthed Black Bass is the most widely used as well as the most distinctive. It is found from Lake Champlain, through the Great Lakes to Manitoba, along the Atlantic slope to South Carolina, throughout the upper Mississippi Valley, and in the lakes of southern Canada.

The size of the Small-mouthed Bass depends largely on the waters it inhabits. Fishes of four or five pounds are decidedly large. There are records of specimens still larger, but the angler of to-day in our overfished streams and lakes is well content with a two-pounder.

The Black Basses defend their eggs on the spawning nests with great vigor and it is the male that assumes this task, the female deserting as soon as the eggs have been deposited. His care is continued for a few days after the young appear, when they begin to scatter.

The Large-mouthed Black Bass has a wider distribution than the Small-mouthed species, especially southward, extending into Florida and other States along the Gulf coast. It is in general more abundant and inhabits more sluggish waters.

In the North the two species are commonly found together. The Large-mouthed species is decidedly larger and in Southern waters sometimes exceeds 12 pounds in weight, but average weights are two or three pounds.

This fish has even more names than its relative, but Large-mouthed Bass serves to identify it wherever the two are found together. As a popular game fish, we are safe in placing it next to the Small-mouthed Bass.

The Black Basses are carnivorous fishes, the young feeding largely on insect life, the adults on fishes, Crayfish, and Frogs. In bait fishing these foods, together with the larger insects and their larvæ, are all used. Expert anglers take both species successfully with trolling spoon and artificial fly.

ROCK BASS (Ambloplites rupestris)

(For illustration see Color Plate III)

Among the native fresh-water fishes living in the Aquarium there are few that adapt themselves more readily to the conditions of captivity than the Rock Bass. In a tank now containing fifteen specimens, mostly of large size, there have been no losses for several years.

The natural range of this fish includes the Mississippi Valley, the Great Lakes, and Lake Champlain drainages, but it has been introduced through fish-cultural operations into many States east of the Alleghenies. Its adaptability to pond cultivation will ultimately extend its distribution.

The methods of the expert angler are not at all necessary for the capture of the Rock Bass. Great numbers are taken by amateur fishers wherever it abounds and during the greater part of the year.

In its feeding habits the Rock Bass is about as omnivorous as any member of the Bass-Sunfish family, to which it belongs. Crayfishes and other fresh-water crustaceans, aquatic insects and their larvæ, Snails, and such fishes as its rather large mouth will admit, all contribute to its natural food supply. If we include the grasshoppers, crickets, grubs, earthworms, and other terrestrial baits used in catching it, the food list might be considerably extended. Fish-culturists have found that this species not infrequently cannibalizes to some extent on its own young.

In addition to the baits already mentioned, the trolling spoon and other artificial lures are used successfully; but the Rock Bass has few of the fighting qualities of the Black Basses, for it soon yields to the pull of the line.

The Rock Bass is a thick-bodied, meaty fish, and a couple of fair-sized ones will fill the pan. There are specimens in the Aquarium a foot long that have nearly trebled in size since their arrival, six years ago. It is known, however, to grow somewhat larger.

At spawning time, late in May, the Rock Bass makes its nest in shallow water along shore, like Basses and Sunfishes generally. The fishes are sociable at this time and their nests are often found in groups close together, which is not the habit with the pugnacious male Black Basses.

CALICO BASS (Pomoxis sparoides) and CRAPPIE (Pomoxis annularis)

(For illustration see Color Plate IV)

The Calico Bass belongs naturally to the region including the Great Lakes and the Mississippi Valley. Being a good food-fish and well adapted to cultivation in ponds, its distribution has been considerably extended by artificial means.

Like other widely distributed fishes, it has several names, one of which, Black Crappie, is sometimes used to distinguish it from its nearest relative, the Crappie or White Crappie. Both kinds are found in the above-named region, but, being of similar appearance, anglers do not always recognize the differences.

The Calico Bass has a relatively deeper body, is darker than the Crappie, and weighs more as compared with a Crappie of the same length. Naturalists easily distinguish them by their dorsal spines, the Calico Bass having seven or eight, while the Crappie has five or six.

The name Calico Bass is suggested by its markings, the Crappie being always paler. Both kinds are found in Western markets. The annual market catch in the Mississippi Valley, of the two combined, sometimes exceeds 1,000,000 pounds. The Calico Bass is chiefly a feeder on aquatic insects and their larvæ. It lives peaceably with other fishes when kept in ponds. So many are taken by anglers that it has been called "the fish for the millions."

If the Calico Basses which have lived in the Aquarium for 10 years continue to thrive in captivity, it will be interesting to see what size they attain with increasing age. Exceptionally large specimens have been reported as exceeding two pounds in weight.

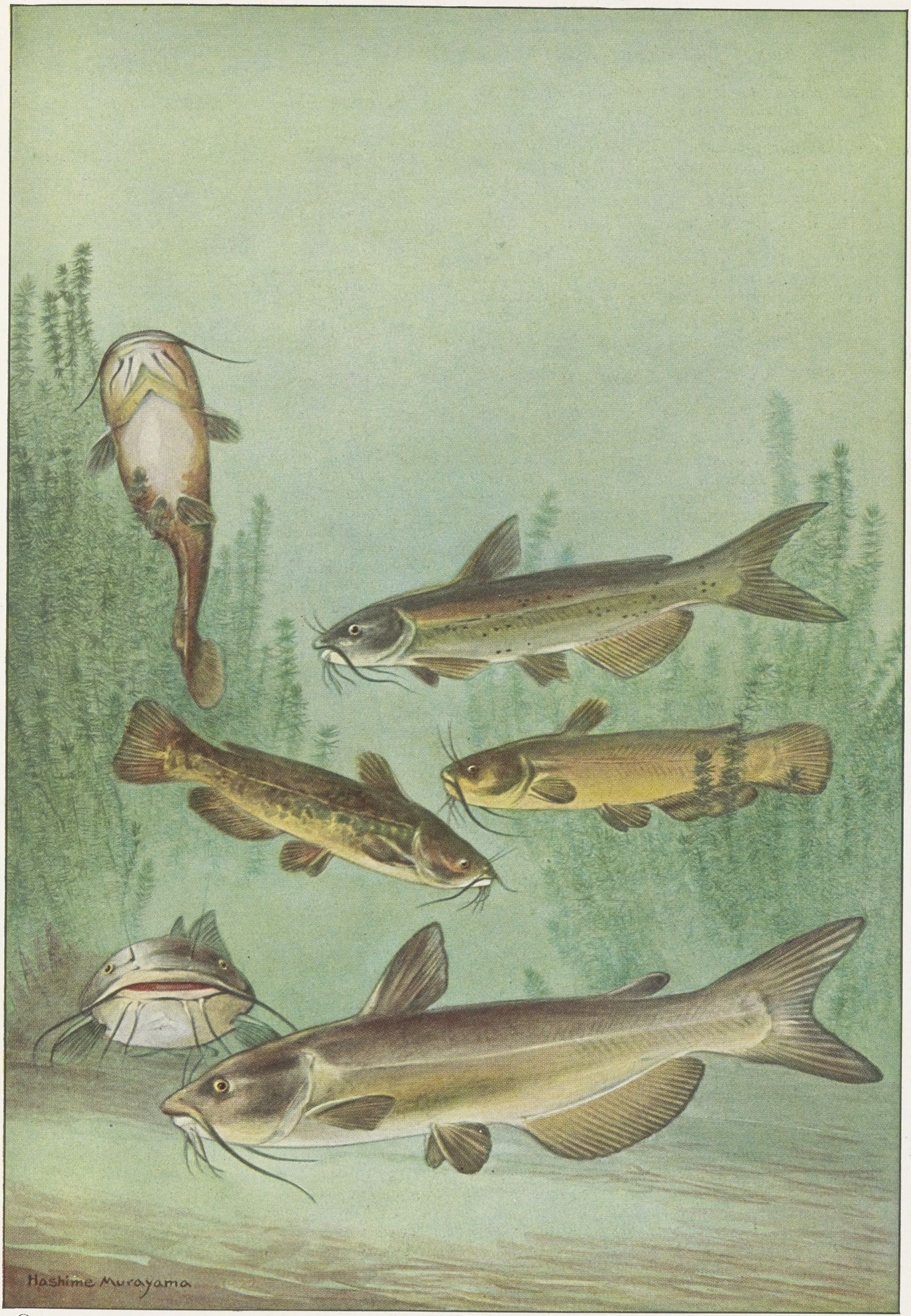
WHITE PERCH (Morone americana)

(For illustration see Color Plate V)

There are few native fishes that live equally well in fresh or salt waters. The White Perch, living chiefly in brackish tidal waters, ranges freely into both. In rivers it passes up beyond all trace of salinity and often becomes landlocked in strictly fresh ponds, where it breeds for considerable periods. On the other hand, it is taken in abundance about coastal islands where conditions are altogether those of the salt sea.

In aquariums it has been kept for long periods in tanks, either fresh or salt, but the best results have been obtained in tanks supplied with both kinds of water. There are specimens now living in such artificially maintained brackish water that are 10 years old. They have reached lengths of 10 to 12 inches and continue to be hardy under the restrictions and the monotonous fare of life in captivity.

Years ago specimens of live White Perch intended for exhibition were obtained from one of the park lakes in New York City where they had been introduced; but, although fully protected, the supply gradually diminished to the vanishing point. It would seem, therefore, that the race cannot breed indefinitely in fresh



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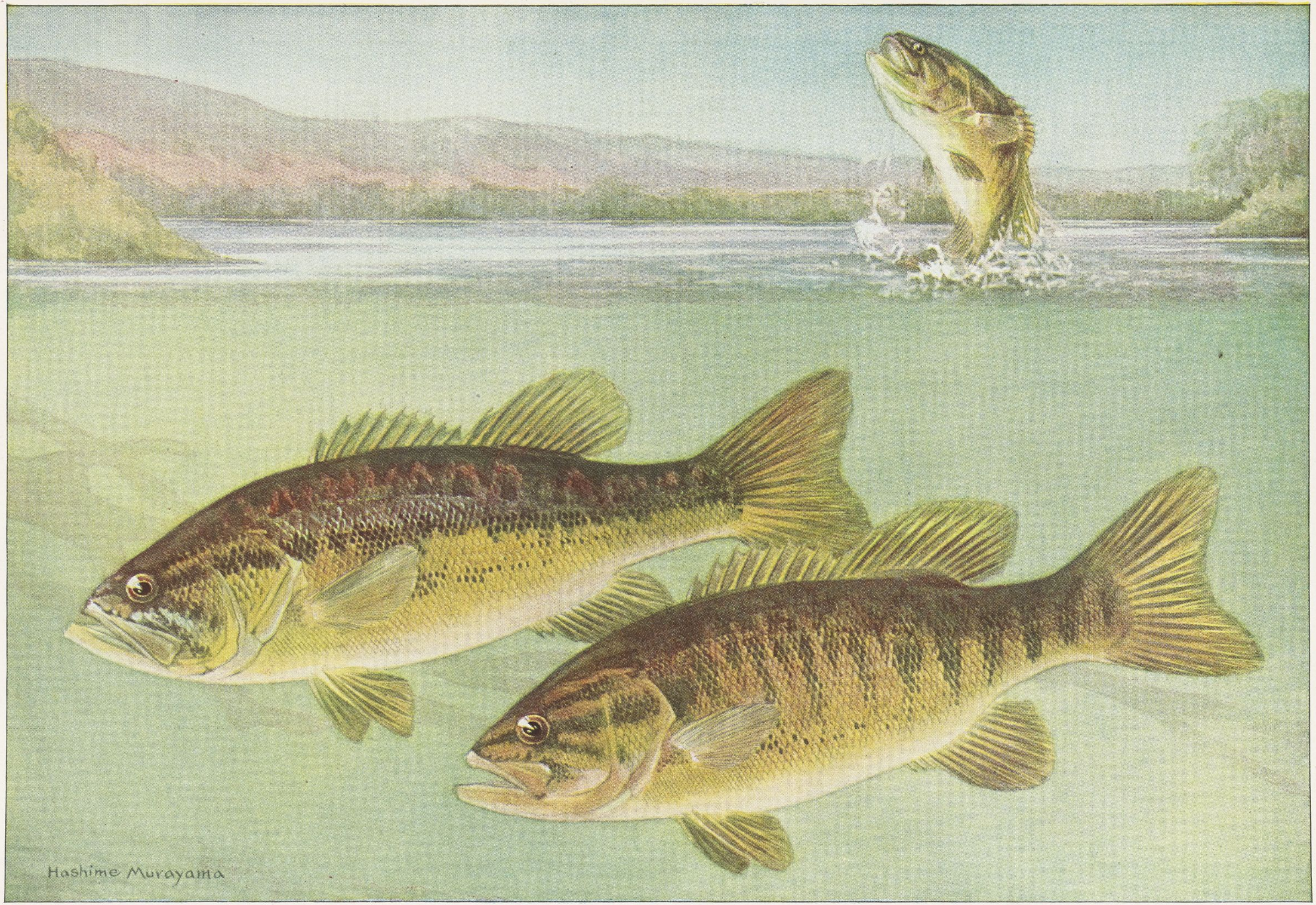
SPOTTED CATFISH (*Ictalurus punctatus*) [at top]; COMMON BULLHEAD (*Ameiurus nebulosus*) [in middle at left], AND OTHER CATFISHES

There are many kinds of Catfishes in our waters, and they are abundant enough to be of considerable importance in the supply of food fishes. The annual catch for market has been known to exceed fourteen million pounds. Great numbers are also taken everywhere with hook and line.



© Painted by Hashime Murayama

LARGE-MOUTHED BLACK BASS (*Micropterus salmoides*) [upper]; SMALL-MOUTHED BLACK BASS (*Micropterus dolomieu*) [lower]

The Black Basses are both well-known anglers' fishes, the Small-mouthed species being by far the gamier of the two. Although closely related, they are easily distinguished by the size of the mouth and by the color pattern; in the Small-mouthed Bass the upper jaw does not extend beyond the eye as in the Large-mouthed species. In the former the color markings tend to form vertical bands, while the latter has a dark stripe along the side.

 Painted by Hashime Murayama

ROCK BASS (*Ambloplites rupestris*)

This fish is well known in the Mississippi Valley and the States bordering on the Great Lakes. It is valued for both food and sport. Great numbers are taken by amateur fishermen wherever it abounds, and it can be caught during the greater part of the year. A couple of fair-sized Rock Bass will fill the frying pan. A name often applied to this fish is "Red-eye."

IV

© Painted by Hashime Murayama

CRAPPIE (*Pomoxis annularis*) [upper]; CALICO BASS (*Pomoxis sparoides*) [lower]

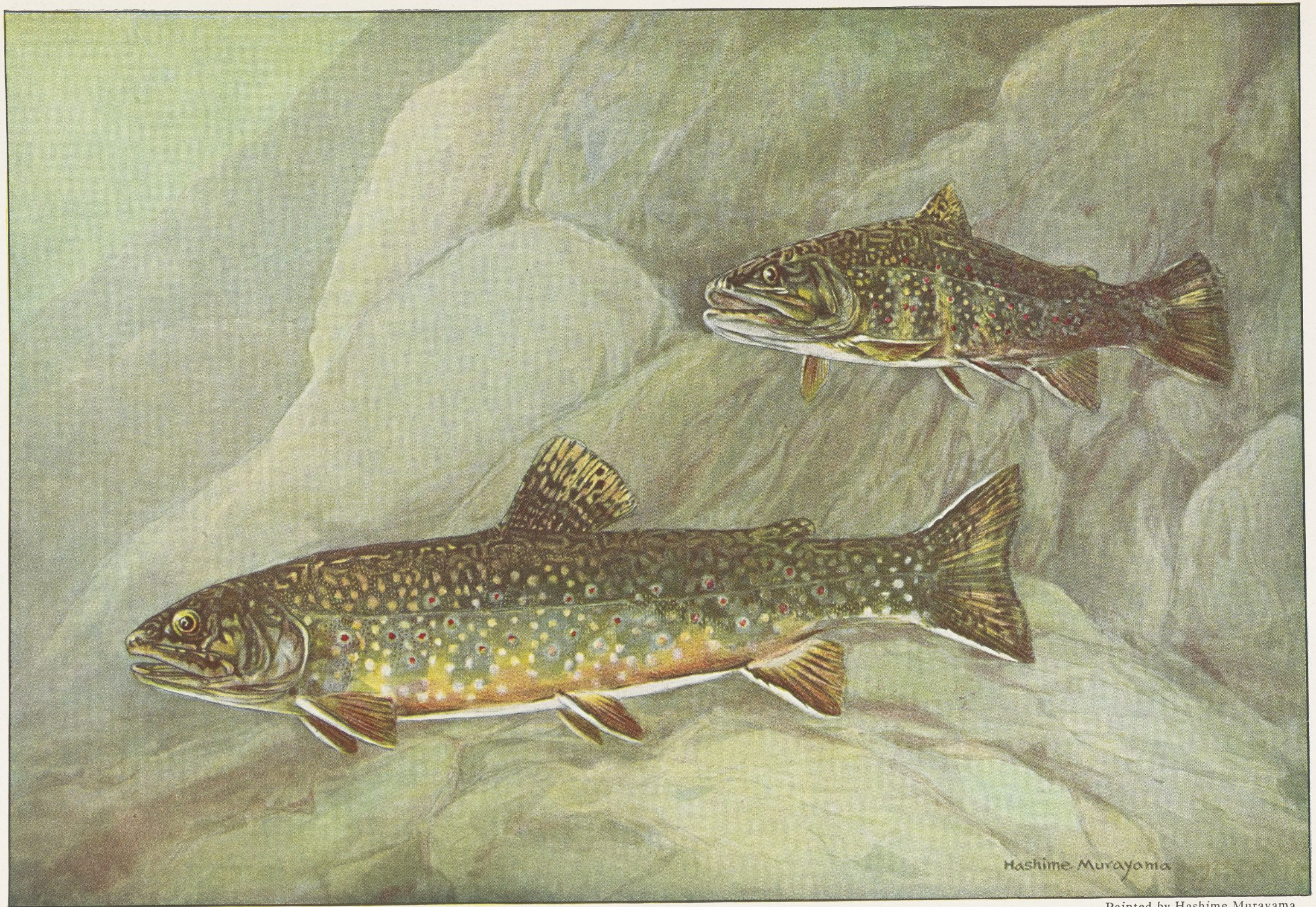
These fishes belong chiefly to the Great Lakes region and the Mississippi Valley. They are much alike in appearance, but the Calico Bass has seven or eight dorsal spines, while the Crappie has five or six. Both are fine sport fishes and both are handicapped with many local names.

Painted by Hashime Murayama

WHITE PERCH (*Morone americana*)

The White Perch belongs to the Atlantic coast region, and is one of the few fishes that live in both fresh and salt waters. It not only ranges far up the rivers, but is taken in abundance by net fishermen along the coast. The White Perch is good eating whether from fresh or salt water and anglers take it with all sorts of baits. It sometimes reaches a weight of two pounds.

VI



Painted by Hashime Murayama

©

BROOK TROUT (*Salvelinus fontinalis*)

This is doubtless America's favorite game fish and the one most written about. It is not only much sought by anglers, but is raised by fish-culturists for the fancy price it brings in the market. Over-fishing, deforestation and water pollution all contribute toward the steady reduction of its numbers and the restriction of its range.

restriction of its range.

VII

© Painted by Hashime Murayama

LAKE TROUT (*Cristivomer namaycush*)

This is the largest of all Trouts, having been known to reach a weight of one hundred pounds. It ranks next to the Whitefish in commercial importance; the total annual catch in the Great Lakes recently exceeded thirteen million pounds. Anglers take many in the lakes of Maine, where it is called "Togue."

VIII

©

Painted by Hashime Murayama

McCLOUD RIVER RAINBOW TROUT (*Salmo irideus shasta*)

The Rainbow has been introduced into most of the Eastern States. It is larger than the Brook Trout and can live in warmer water. Although anglers do not consider it quite so gamy, it is a valuable sport and food fish, especially useful in stocking waters no longer suitable for Brook Trout.

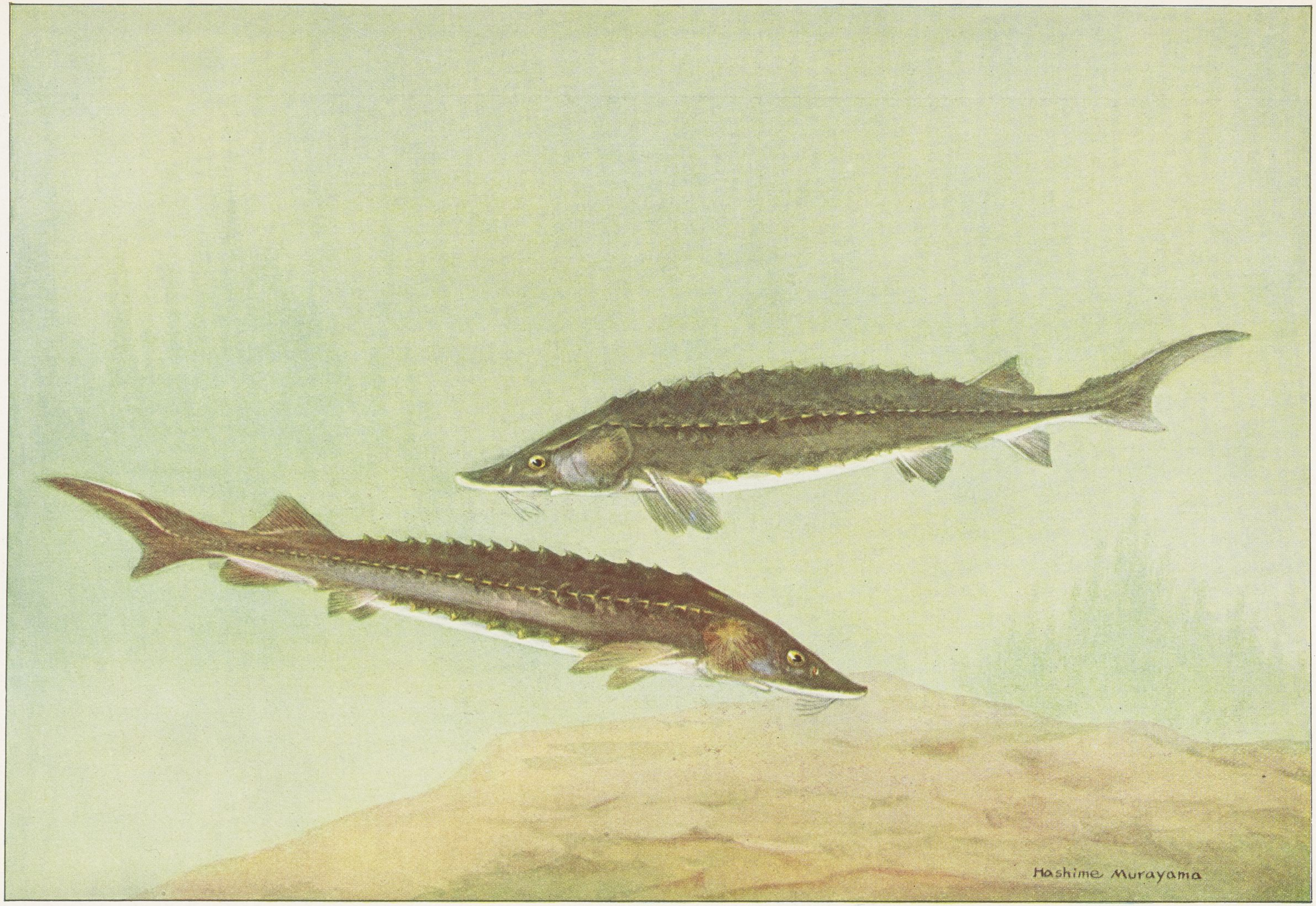
IX

©

Painted by Hashime Murayama

PIKE (*Esox lucius*) [upper]; EASTERN PICKEREL (*Esox reticulatus*) [lower]

The Pike of North America is probably not distinct from the Pike of the Old World. Specimens have been taken weighing over forty pounds. The Eastern Pickerel is the largest of our three species. Both Pike and Pickerel are valued as food and game fishes and like the Muskellunge are exceedingly voracious.



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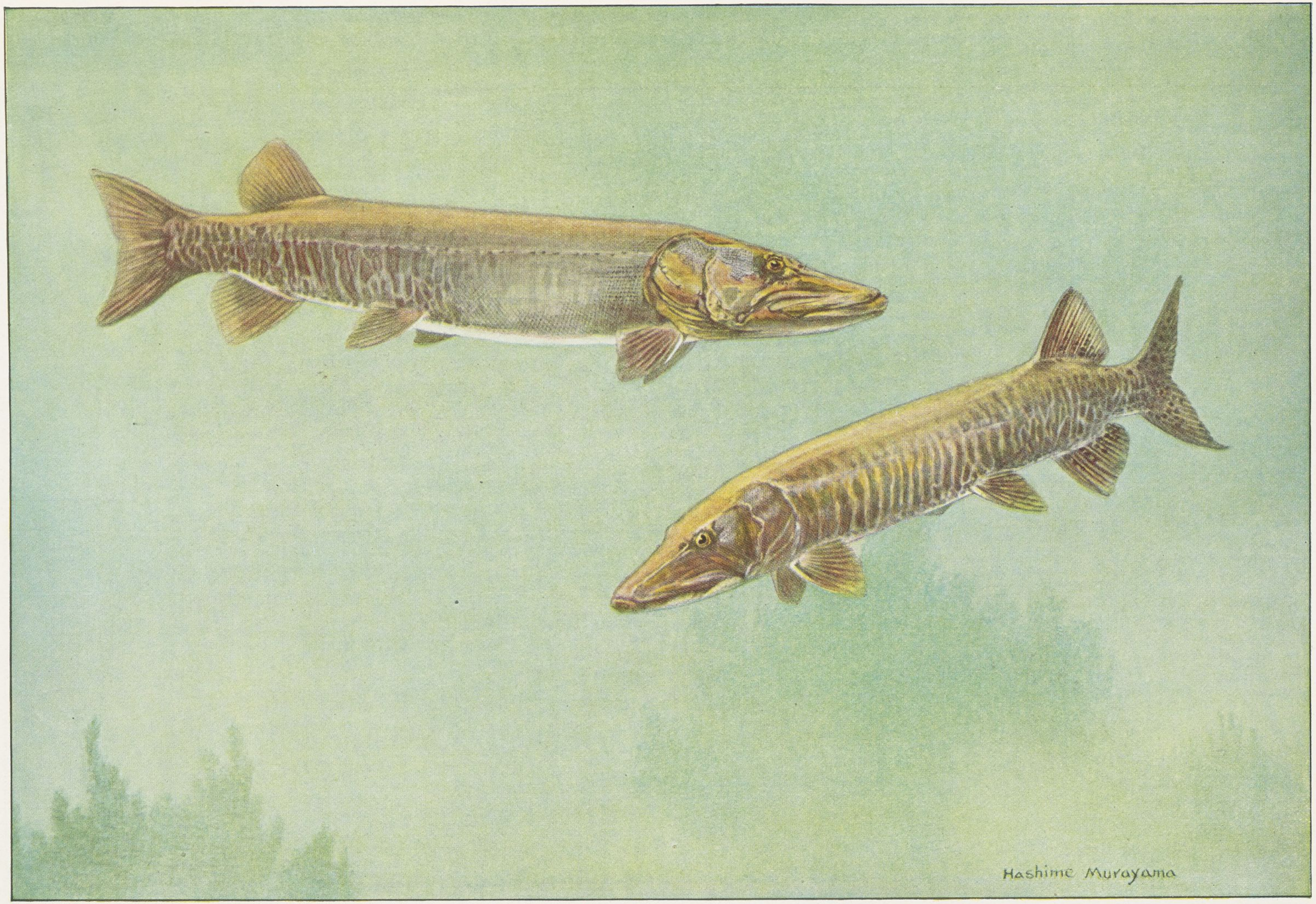
LAKE STURGEON (*Acipenser rubicundus*)

The history of the Sturgeon is a story of wanton waste. When the fisheries of the Great Lakes were first being exploited, the Sturgeon was destroyed as useless. Now that its great value is recognized, it may be too late to save it from extinction, as fish-culturists have not been able to solve the problems connected with its propagation. The Sturgeon is valued chiefly for the caviar made from its eggs.



Painted by Hashime Murayama

LAKE CHAUTAUQUA MUSKELLUNGE (*Esox ohiensis*)

There are three species of Muskellunge, the one shown here inhabiting Lake Chautauqua and the upper Ohio River system. All are Northern fishes, much alike in habits. The Muskellunge is the largest of the Pike family and in the Great Lakes has been known to exceed eighty pounds in weight. It is celebrated as a game fish having both size and strength. In bringing to gaff a large Muskellunge, the angler must put all his dexterity into full play.

Painted by Hashime Murayama

COMMON WHITEFISH (*Coregonus clupeiformis*)

This is one of the most abundant and valuable of our food fishes, and with other Whitefishes one of the most important fresh-water fishes in the world Over twelve million pounds of Whitefish have been taken in the Great Lakes in a single year. The Whitefish is the subject of extensive propagation by the Government.

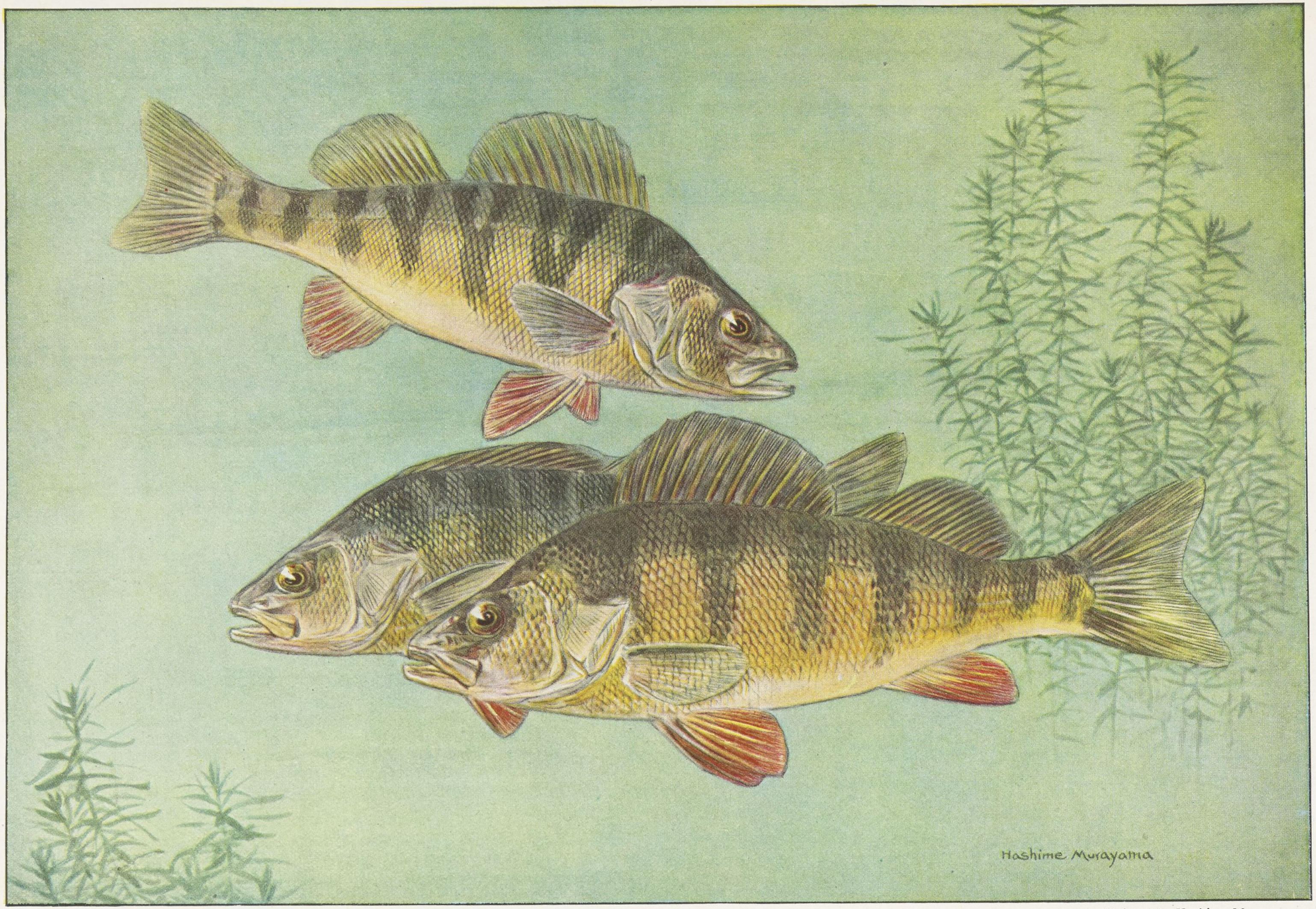
XIII

Painted by Hashime Murayama

FRESH-WATER DRUM (*Aplodinotus grunniens*)

This large fish of the Great Lakes and the Mississippi Valley is of considerable importance in the market fisheries, but of little interest to anglers except in the South. It is related to the Sea Drum and makes the same drumming sounds. It has heavy grinding teeth like the sea variety and feeds chiefly on Mollusks and Crayfish. Anglers take it best with Crayfish bait.

XIV



© Painted by Hashime Murayama

YELLOW PERCH (*Perca flavescens*)

Found throughout the Northern and Eastern States, this is one of our best-known fishes. It is caught by anglers of all ages, and great quantities are taken for market with nets. Among the commoner fishes there is none of better flavor. It comes as near being everybody's fish as any other.

XV

© Painted by Hashime Murayama

SAUGER (*Stizostedion canadense*) [upper]; PIKE-PERCH (*Stizostedion vitreum*) [lower]

The Pike-perch, often called "Wall-eyed Pike," belongs to the Perch family, although its form is suggestive of the Pikes. It has been known to reach a length of three feet. In commercial importance, it ranks next to the Whitefish and the Lake Trout, millions of pounds being taken in the net fisheries of the Great Lakes. Anglers find the Pike-perch a good game fish. The young are liberated from Government hatcheries by hundreds of millions. The Sauger has the same northerly distribution as the Pike-perch. It resembles it in appearance, but is smaller and of less commercial importance.

Painted by Hashime Murayama

COMMON EEL (*Anguilla rostrata*)

The Eel is a fish that spends its long life in fresh water, descending to the sea in old age to spawn but once and die. For centuries its mysterious ways have puzzled naturalists who have discovered recently that it spawns near the Bermuda Islands in deep water, the transparent larval Eels not seeking the rivers until a year old, when they appear as Elvers working upstream.

waters, but must renew its fertility through occasional baths in the vitalizing sea.

Complete exclusion from the brackish or fresh waters, where it spawns, would doubtless lead to extermination as readily as long-continued imprisonment in absolutely fresh water. According to the records of anglers, the largest specimens are those taken in salt or brackish waters.

The White Perch belongs to the tidal region of the Atlantic coast from Nova Scotia to South Carolina. It is abundant around Long Island and in the Hudson River up as far as Albany. It is taken through the ice in the Hudson, where it is present throughout the year.

It is equally abundant in the Delaware and Susquehanna rivers and Chesapeake Bay, ranging well upstream, and is commonly taken in pound and fyke nets along the coast.

In North Carolina the annual catch amounts to 1,000,000 pounds. Anglers catch it in abundance and net fishermen keep the markets well supplied with it. Fishery statistics show that the market catch along the Middle Atlantic States sometimes amounts to 2,000,000 pounds a year.

The White Perch is good eating, either from fresh or salt water. Hook-and-line fishers find Shrimp bait the best, but it responds readily to Minnows, young Eels, small Crabs, or any of its natural foods. Specimens of two or three pounds are reported from the eastern end of Long Island. In fresh waters, worms, grasshoppers, and other insects are effectively used.

The White Perch rises to the fly, especially in fresh waters, and resists bravely when hooked. A fish a foot long weighs about two pounds, but this is larger than the average.

It is a gregarious species, usually frequenting the shallower waters along shore. Spawning begins soon after the ice leaves and lasts a couple of months. Females have been taken with eggs as late as June 10. Fish-cultural experiments have shown that the eggs can be hatched artificially in from three to five days.

Considering the adaptability of the White Perch to the conditions of captivity, especially in brackish water, there is reason to suppose that it will receive more attention from fish-culturists than it has in the past. Anglers would know it better if its range extended farther inland.

BROOK TROUT (Salvelinus fontinalis)

(For illustration see Color Plate VI)

The Brook Trout is the favorite game fish of America. Originally found from Labrador westward to the Saskatchewan and southward along the Alleghenies to Georgia, it has been carried by fish-culturists to the Rockies, the Sierras, the upper Mississippi Valley, and wherever rapid streams of suitable temperature are found.

It has almost disappeared from lowland streams in the North, which have become unsuited to it as a result of deforestation and water pollution.

The Brook Trout persists in small coastal streams where the conditions favorable to it have not been disturbed, and it often descends to brackish water. It will live in streams having a summer temperature as high as 70°, provided they have swift currents.

The Brook Trout cannot live through the summer in the New York Aquarium without the aid of refrigerated water, although the city supply is derived in part from the Catskill Mountains and flows 100 miles underground. The Brook Trout will live in cool lakes and ponds, but cannot reproduce in such situations without access to the gravelly beds of running brooks at spawning time.

Trout culture in America dates back to the early fifties. Fish-culturists raise great numbers of Brook Trout, both for market and for distribution in small artificial ponds, by feeding the fishes and caring for the eggs in hatchery troughs provided with flowing spring water.

The instinct to move upstream is very strong in young Trout; when a miniature "fishway" with its stairs of tiny box pools is connected with a hatching trough, they will promptly begin to ascend and cannot, in fact, be kept down while water is allowed to flow through it.

The Brook Trout spawns in the fall, when streams begin to cool, but the eggs do not hatch out until springtime brings higher temperature. The hatching period lasts from three to six months, according to latitude and altitude. The Brook Trout spawns when two years old. Larger and older fishes deposit from 500 to 2,000 eggs.

In lakes where there is an abundant food supply, the Brook Trout has in the past been known to reach the rare weight of 10 pounds; but to-day, when thousands of anglers are whipping the Trout streams, a one-pound Trout is a large one. Many good Trout waters have been ruined by the ill-advised introduction of predatory fishes.

The coloration of the Brook Trout is extremely variable. In some waters the fish may exhibit all the brilliancy of which it is capable, while in another watershed not far away it is so dark that but little color is discernible.

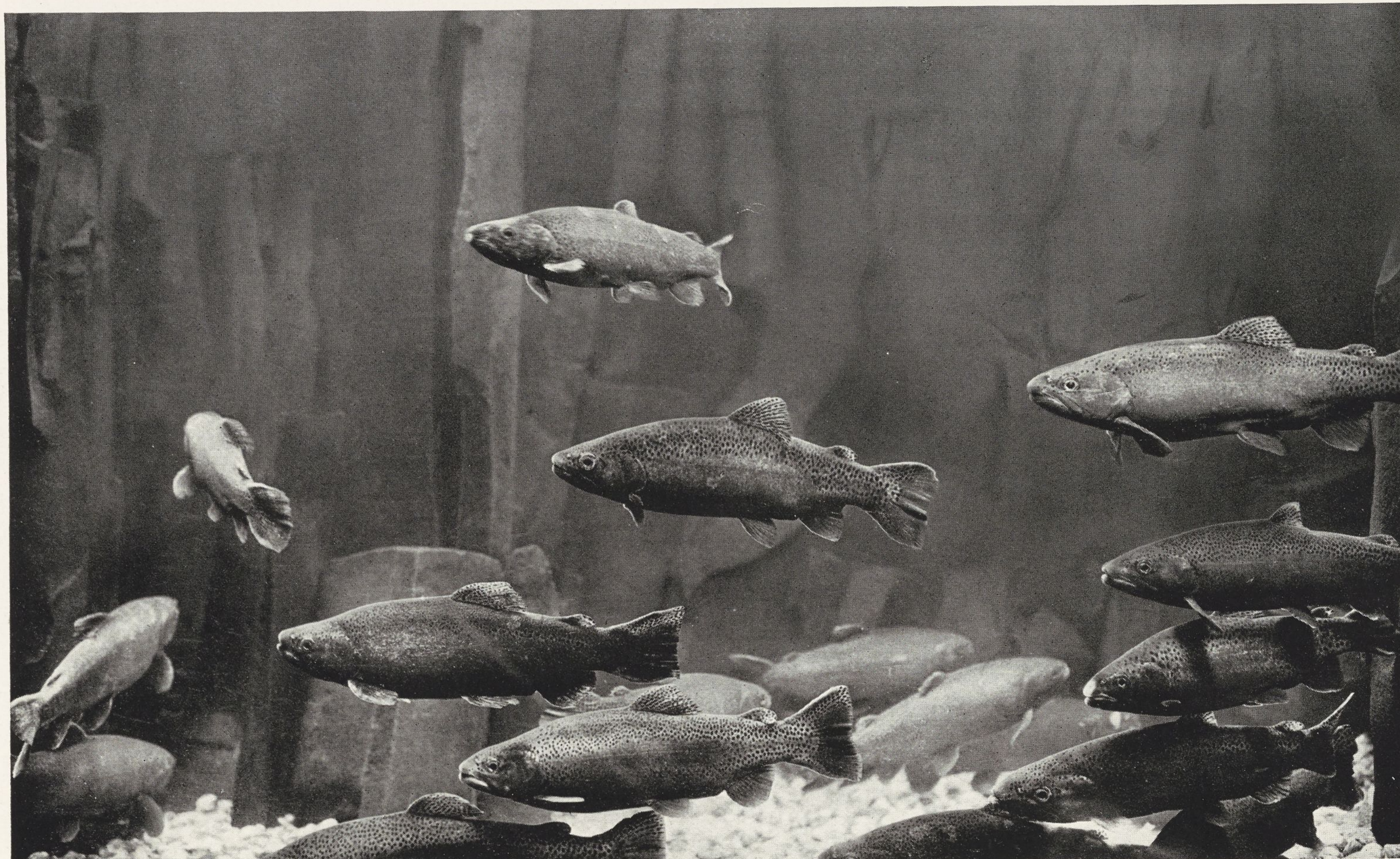
A notable illustration of this is found on Long Island, the Trout on the south side of the island being among the showiest of the species, while those of the north side are as dark as the Brook Trout ever becomes, although the supply on both sides is maintained by hatchery-raised fishes. After a few months in captivity, the bright colors of the former tend to disappear, while the latter become somewhat paler. This may be due largely to a change in diet and the exclusion of direct sunlight from the tanks.

In the Trout, as in many other fishes, the colors vary with age.

In streams the Brook Trout is largely a feeder on aquatic insects, while in lakes and ponds it feeds much on small fishes. In the Aquarium it subsists cheerfully on chopped fish, like the other captives of the tanks, and in the average hatchery pond becomes a fat liver-fed gourmand.

The Brook Trout is not a leaping fish, like the Bass, when hooked, although it may rise clear of the surface in striking the fly.

We need not describe methods of capturing the Trout; anglers have been writing of this in great detail since the days of the Father of Anglers. No native game fish is more worthy



Photograph by E. R. Sanborn

A STRONG FIGHTER ON THE LINE: McCLOUD RIVER RAINBOW TROUT

This McCloud River variety is the stock from which our introduced California Rainbow Trouts were derived. It is more given to leaping than the Brook Trout.

of protection in the waters still suited to it than the Brook Trout.

LAKE TROUT (Cristivomer namaycush)

(*For illustration see Color Plate VII*)

The Lake Trout of the Great Lakes belongs chiefly to the fish trade. In these inland seas the angler's share is small in comparison. It is the largest of all Trouts and is known to have reached a weight of 100 pounds. The average of those taken in the gill nets used at the present time weighs less than 10 pounds, while those caught by anglers along shore average but half that weight. The writer once accompanied a northern Alaska expedition, a member of which brought into camp specimens of this Trout exceeding three and a half feet in length. They were taken in a large lake at the headwaters of the Kowak River, above the Arctic Circle, where they were very abundant.

Among our fresh-water fishes the Lake Trout ranks next to the Whitefish in commercial importance. It is found throughout the Great Lakes and from there northward, in all the large lakes of British America and Alaska.

A deep-water form of this Trout, called Siscowet, is taken in great numbers in Lake Superior, the gill nets being set at times in depths exceeding 500 feet and lifted by steam power. The writer once made a cruise north of the Apostle Islands on a steam fishing boat operating 40 nets, each 600 feet long. These were set in one "gang," constituting a single net more than four miles in length.

Each deep-water fishing boat attends to four or five of these great nets. As the net is lifted by the windlass forward, it is carried aft in sections, put together again, and paid out over the stern. The nets were about eight feet wide, with four and a half inch mesh.

The largest of the deep-water Lake Trout taken by our vessel was two feet ten inches long and weighed 21 pounds.

It would be interesting to know the greatest depth at which Lake Trout have been taken, as Lake Superior, one of the deepest lakes in the world, has depths exceeding 1,000 feet and its bottom is far below sea-level.

Some time later a day was spent on a steam fishing boat in the Georgian Bay near its connection with Lake Huron, and the lifting of a gill net six miles in length was observed. It was set at a depth of 100 feet and the work of lifting and resetting occupied five hours. The catch was nearly 1,000 pounds of Lake Trout, the largest of which was three feet long and weighed 15 pounds.

There are many steam vessels in the Great Lakes engaged in such wholesale fishing, as long as the Lakes are free from ice. The annual net catch of Lake Trout in the Great Lakes in 1917 exceeded 13,000,000 pounds.

The writer has taken Lake Trout in the Georgian Bay at depths of about 50 feet with hand line and trolling spoon, but the sport would have been better had rod and reel been used. Anglers who have used the rod with 300 feet of line and Minnow bait find that the fish can be played in a satisfactory manner.

Surface trolling, when the Trout are found in shallower waters, affords better sport. In smaller and shallower lakes, like those of Maine, where summer water temperatures are higher than in the Great Lakes, the Lake Trout is often taken with the fly. In Seneca Lake, in New York State, it is taken with a special trolling rig designed to play the spoon 10 or 20 feet under the surface.

The Lake Trout is easily distinguished from other Trouts by the numerous small, pale-yellowish spots which cover its body from head to tail. It is a voracious fish. Forbes tells of a 20-pound Lake Trout which had 13 good-sized Lake Herring in its stomach.

Lake Trout fry are turned out by the fish hatcheries in great numbers. The spawning season varies in different lakes. Five or six thousand eggs are stripped from fishes of ordinary size, but large specimens yield many more. The eggs hatch in from two to three months.

The Lake Trout endures captivity very well; the Aquarium has 20-inch specimens received in 1919, some of them perfect albinos with bright pink eyes.

Several names are applied to the Lake Trout, one of which is Mackinaw Trout. In the lakes of Maine it is called Togue, while in Canadian lakes it goes by the Indian name Namaycush.

McCLOUD RIVER RAINBOW TROUT (Salmo irideus shasta)

(*For illustration see Color Plate VIII*)

The Rainbow Trout belongs to the Pacific slope of the Sierras and Cascades; wherever it is found to the eastward of these ranges it is an importation.

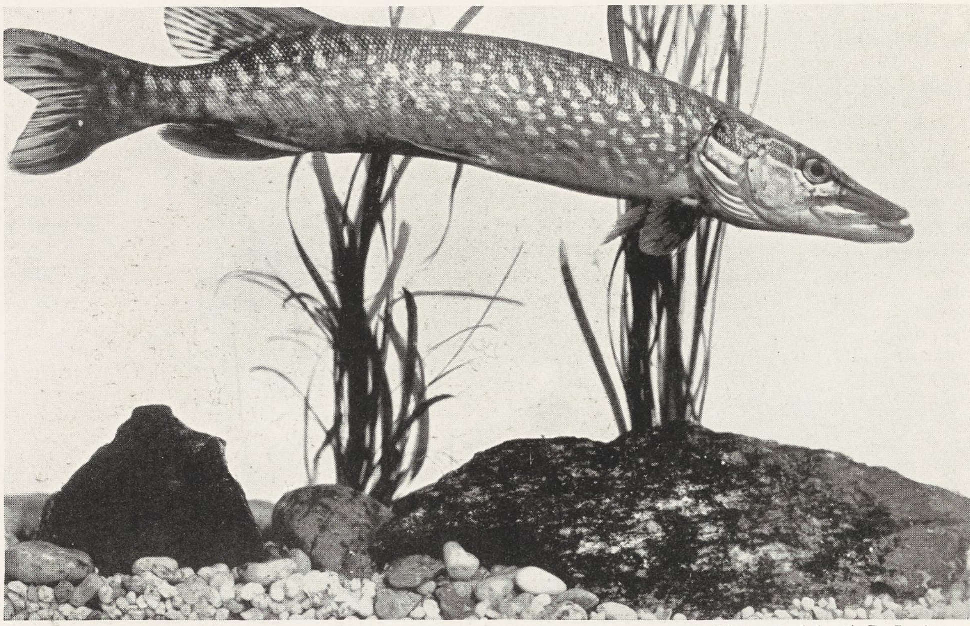
There are several geographic races of this Trout, the one now found in Eastern streams and lakes being the northern California variety, *Salmo irideus shasta*. Commencing in the early eighties, the original stock was widely distributed from the Government hatchery on McCloud River south of Mount Shasta. It was the writer's good fortune to be attached to this station years ago and to participate in its work.

The acclimatization of this fish in other parts of the United States and in foreign countries is one of the notable successes of modern fish culture. Taken to New Zealand in the late eighties, it soon became well established there.

The introduction of the Rainbow Trout in Eastern States provided a substitute for the Brook Trout in many waters which had become unsuitable for that species, as a result of advancing civilization.

While generally not as large in the East as in its native Sierra streams, it has in certain favorable localities been found even larger. It can endure warmer water than the Brook Trout and live farther downstream than that species. In streams near the sea it often lingers in brackish water.

While the Rainbow Trout is a springtime spawner on the Pacific slope, depositing its eggs from February to May, it has in its Eastern habitat adapted itself to the very different



Photograph by E. R. Sanborn

THE PIKE, A FRESH-WATER MARAUDER

The habits of the Pike are similar to those of the Muskellunge. It tries no tricks when hooked, but reels off the line as though relying on its sheer strength to get away.

climatic conditions prevailing there and now spawns in the fall and early winter, like the Brook Trout, but the eggs hatch in less time.

The vitality of the artificially fertilized eggs has made it possible to ship them to great distances in a half-incubated condition, after which the hatching process can be completed by ordinary fish-hatchery methods. In this way fertilized eggs of the Rainbow Trout have been sent to the Atlantic coast, to Europe, and even to New Zealand in refrigerated packages with but little loss.

This is the method now used in distributing not only Trouts and Salmons, but many other kinds of fishes.

Eastern anglers do not usually rate the Rainbow with the Brook Trout as a game fish, but we cannot believe that this criticism applies in its native rivers. It is, perhaps, true that it is there a better food fish. Anglers have their own ideas on such matters, and are not to be dissuaded from opinions formed in places where they have enjoyed good sport.

In the McCloud River we have taken three- and four-pound specimens, but the average is smaller. It is known to attain a weight of 10 pounds, especially when transplanted to warmer waters, or where the food supply and the large area of a lake provide conditions favoring greater growth.

It is probably not so gamy a fish in warm waters as in mountain streams. We have seen it leap repeatedly when hooked—a thing the Brook Trout seldom does.

The Rainbow is a fine sportsman's fish, taking the fly much like other Trouts, and is not a competitor of the Brook Trout in maintaining a place in the wider habitat now afforded it.

In some localities the identity of the Rainbow is confused with that of the Steelhead (*Salmo gairdneri*), also a Pacific coast fish, which has been successfully acclimatized in streams flowing into Lake Superior, Lake Michigan, and elsewhere. It has smaller scales than the Steelhead. In California the Rainbow is not inclined to seek the sea like the Steelhead, while the latter ranges far inland at spawning time, like the Salmon. A few Steelheads have been taken in the McCloud River 300 miles from salt water, and it is not unlikely that some of the Steelhead eggs were unwittingly shipped from there with eggs of the Rainbow.

With its broad, iridescent, purplish-red band along the side, the Rainbow Trout is well named.

EASTERN PICKEREL (Esox reticulatus)

(*For illustration see Color Plate IX*)

The Eastern Pickerel—the largest of our three species—belongs chiefly to the region east of the Alleghenies, from Maine to Florida. It reaches a length of two feet and a weight of seven or eight pounds. Two or three pounds would be near the average size, which varies, however, with the locality.

Chain Pickerel is a name much used in the North, while Jack is more common in the South. It is often confused with the Pike in waters where both are found.

Like others of the family, it leads a solitary life, except at spawning time. Pickerels captured by bait trolling in New Jersey lakes have been taken in rather shallow places, where they found shelter among water plants. Here also the Pickerel deposits its spawn. The eggs are thrown off in long masses like those of Perch and are usually seen among submerged brush and weeds. In the North it spawns in April and May; in the South it spawns earlier and grows faster.

The Pickerel stays in deeper water in winter and is then taken through holes cut in the ice.

It is said that in ponds devoted to fish culture a Pickerel five years old may be a foot and a half long and weigh two pounds, but rapidity of growth depends upon the abundance of food.

The Pickerel will seize a fish half as large as itself and swallow it by degrees.

All fishes of the Pike-Pickerel family are taken by similar methods. Fishes and Frogs are good live baits and are used in trolling, casting, and skittering and artificial lures are used in the same ways.

"Skittering" is an angler's term; it is done with a long rod and a short line, by jerking the bait along the surface.

The Eastern Pickerel is probably a better game fish than either of the other Pickerels. These fishes, being rather easily caught, both in summer and winter, soon become reduced in numbers in the smaller water areas.

Photograph from U. S. Bureau of Fisheries

THE MAGNIFIED SCALE OF A DOG SALMON

This scale was taken from a mature male in its fourth year. Note the "rings," like those of the cross-section of a tree, by means of which the age of a fish can now be computed (see text, page 127).

Another species, the Banded Pickerel (*Esox americanus*), also limited to the region east of the Alleghenies, is smaller than the Eastern Pickerel, seldom exceeding a foot in length. It inhabits chiefly lowland streams and swamps, often descending streams to brackish water.

The Little Pickerel (*Esox vermiculatus*) has a shorter body and longer head than its relatives. It is a fish of quiet waters and does not exceed a foot in length. It belongs to the Ohio and Mississippi Valleys and to streams flowing into the Great Lakes.

PIKE (Esox lucius)

(*For illustration see Color Plate IX*)

The Pike reaches but half the size attained by the Muskellunge. It has much the same distribution but a greater range northward. The writer has taken it above the Arctic Circle in Alaska.

The American Pike is probably not distinct from the Pike of the Old World, but the latter is believed to be larger. Being more widely distributed and abundant than the Muskellunge, it is better known to anglers and is of more economic importance.

The Pike, like the others of its family, is one of the notoriously voracious fishes, destroying great numbers of other fishes and many water birds and small aquatic mammals. It is well equipped for the predatory life and is believed to eat about a fifth of its own weight daily. There is no doubt about its being the enemy of all fishes inhabiting the shallower waters. Only a few Pike can find subsistence in ponds and lakes of limited extent.

Photograph by E. R. Sanborn

THE CALICO BASS DERIVES ITS NAME FROM ITS MARKINGS

This fish is neither large nor noted for gameness, but it is the object of a vast amount of angling over a considerable part of the country. Market fishers take large numbers in the Mississippi Valley.

It is not a suitable fish for propagation in waters adapted to other fishes that are less piscivorous, and its cultivation should be restricted to such localities as are best adapted to it alone, and where it may subsist on fishes of the least value as game or food.

The Pike reaches a length of four feet and a weight of 40 pounds or more. There are several much-quoted records to the effect that the Pike of Europe and Siberia have been known to exceed 100 pounds in weight. Natives of the Alaska Peninsula told me repeatedly that Pike of enormous size inhabit Lake Iliamna.

It may be that the Pike attains its greatest size in far northern waters. In northern Alaska we found it abundant in all parts of the Kowak and its tributaries, especially in quiet lagoons leading off from the river. There were many lurking in shallow water among overflowed mosses, where we continually startled them in walking along shore.

Having little time for angling, we took such Pike as were needed for food by shooting them as they lay in the shallows with hardly enough water to cover them. This was early in August, when the cold Arctic streams are about as warm as they ever get, and the Pikes were probably spawning. In our Northern States they spawn soon after the ice leaves, and the eggs hatch in about three weeks.

The annual yield of Pike and Pickerel in the net fisheries of the Great Lakes exceeds 2,000,000 pounds. The identity of the Pike is often lost in the name Pickerel, with which it is associated in much of its geographic range.

An inhabitant of the shallower waters in summer, the Pike in winter seeks greater depths, doubtless following its food supply, and is taken on baited hooks set through the ice. In summer it is a solitary still hunter, lurking about the edges of weedy or brushy places. It is taken with all sorts of live and artificial baits, in trolling, casting, and skittering.

Many anglers consider Pike and Pickerel fishing a high form of sport and value them also as food-fishes, but there are others who think differently. We have enjoyed them both on the line and in the pan.

LAKE STURGEON (Acipenser rubicundus)

(*For illustration see Color Plate X*)

The Lake Sturgeon is the largest fish of the Great Lakes and, next to the Paddle-fish and the Giant Gar of the Mississippi River, our largest fresh-water fish. It never reaches the great size of the Sea Sturgeons ascending rivers of the Atlantic and Pacific coasts. Milner, who examined many in the early seventies, saw none longer than six feet, but found reports around the Lakes of larger Sturgeons. In 1922 a Sturgeon was taken in Lake Huron which measured seven feet three inches and weighed 225 pounds.

The history of the Sturgeon is a story of wanton waste. In 1872 Milner reported a fishing firm at Sandusky, Ohio, engaged in preparing smoked Sturgeon and caviar, which used from 10,000 to 18,000 Sturgeons a year. Before this firm began to utilize them the local catch of Sturgeons, which were always present in the nets, was destroyed as useless. This was also the practice elsewhere on the Lakes.

When the value of the fish was finally recognized, its decimation proceeded so rapidly that it soon became scarce and has been so ever since.

The difficulties encountered in the propagation of the Sturgeon by artificial methods have so far been only partially overcome. The breeding sizes available for experimental fish-culture are now so limited that extermination is feared.

In 1880 the catch of Sturgeons in the Great Lakes exceeded 7,000,000 pounds. In 1917 it had fallen to less than 100,000. In the upper Mississippi River and its tributaries the catch has fallen in proportion.

The Sea Sturgeons have also decreased at a rapid rate and fish-culture has made little progress in propagating any of them.

When we consider that the caviar alone from a single large female Atlantic Sturgeon is worth nearly $100, it is easy to realize what the passing of this fish means. Such is the rate at which we are harvesting our wild crops.

The Lake Sturgeon inhabits also the large interior lakes of British America, but statistics on the yield from those waters are not at hand. The small Shovel-nosed Sturgeon of the Mississippi River, belonging to a different genus, is of much less value commercially.

The Lake Sturgeon is inoffensive as far as other fishes are concerned, except as it may disturb their eggs, being strictly a bottom feeder and living on mollusks, crustaceans, worms, and more or less small plant life. Its mouth, devoid of teeth and placed on the under surface of the head, is suckerlike in form and can be protruded downward like those of Suckers. The heavy snout is used for stirring up the bottom.

Sturgeons have lived only two or three years in the Aquarium, but doubtless would live longer in captivity were it practicable to keep them in mud-bottomed pools and supplied with their natural foods. Unfortunately, aquatic animals confined under the conditions now practiced are compelled to subsist, especially in winter, on such foods as the markets afford.

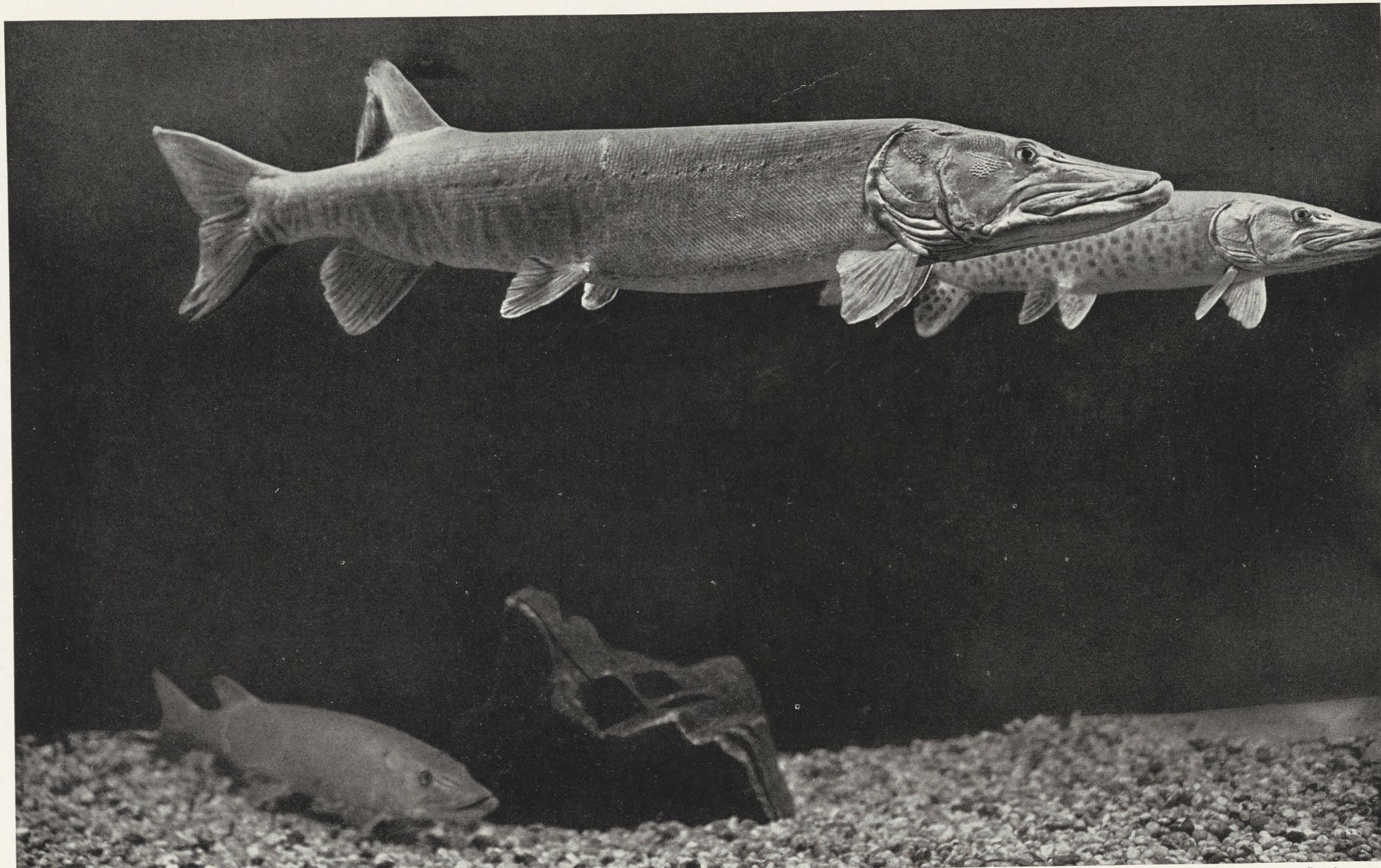
The Sturgeons are fishes of ancient lineage, the species having been more numerous in former ages, when they were more heavily armored with bony scales than are those now existing. All Sturgeons are at once distinguishable by their five longitudinal rows of heavy, bony scales.

The Sturgeon is an active fish, often leaping clear out of the water. It lives chiefly in the shallower waters along shore, where it spawns in June.

MUSKELLUNGE (Esox masquinongy)

(*For illustration see Color Plate XI*)

There are so many ways of spelling the Indian name of this fish that we have adopted the one apparently most in use, only after an orthographical search which revealed 24 ways of spelling it. The Muskellunge is the largest of the Pike family, being known to exceed 80 pounds in weight, while 40-pound specimens are fairly common.



Photograph by E. R. Sanborn

THE BIG AND POWERFUL MUSKELLUNGE, MOST VORACIOUS OF FRESH-WATER FISHES

This fish lies half hidden, in wait for his victim. His habit of motionless poise makes him a good subject for the camera.

It is a northern fish, inhabiting mainly the Great Lakes, Lake Champlain, Lake Chautauqua, lakes of Canada, the St. Lawrence River, and the upper Mississippi and tributaries.

It is celebrated as a game fish, having both size and strength. Unless equipped with a rod suitable for a large specimen, the angler may have to play the fish an hour before landing it.

Live bait casting and spoon trolling are the usual ways of taking the Muskellunge.

As a fish-eater the Muskellunge rivals the Barracuda of salt water, making the same fierce rushes and having a similarly large mouth set with dangerous teeth. There is, in fact, a superficial resemblance between these two widely separated fishes.

With a long, narrow body, strong dorsal and anal fins placed far back on the body, and a powerful tail, the Muskellunge is well equipped for speed. It has the look of a three-propeller craft, but the power is reserved for sudden bursts of speed, as it is not given to ranging far from its customary lair. The Muskellunge like other fishes of the Pike family, is solitary in habit, lurking in sheltered spots, whence it darts upon its prey.

As food-fishes, neither the Muskellunge nor the other Pikes are usually rated as high as the Trouts and Basses.

The Muskellunge with which we are best acquainted is the species belonging to Lake Chautauqua and the upper Ohio River system—*Esox ohiensis*. This species has long been on exhibition in the Aquarium, where 30-pound specimens have lived four or five years at a time and would have lived longer but for accidents to the water supply. Although well fed, they have occasionally attacked their large tank mates, inflicting serious injuries. It is sometimes called Barred Muskellunge. Mr. G. A. Winchester states that the largest specimen taken in Lake Chautauqua weighed 49 pounds. Forty-pounders are taken every season, but seven pounds is about the average for that lake. A 42-pound specimen was taken in Lake Chautauqua which had a length of 52½ inches (see page 127). In this lake it is taken in summer by spoon trolling. In the autumn live baits—Suckers, Shiners, and Creek Chubs—are used.

Live-bait fishing is more effective at night and attracts larger fish. Skittering with dead Minnows is fairly successful in summer and both casting and skittering can be done over weedy areas. A good day's catch would be five or six fish. The State hatchery at Lake Chautauqua, between 1896 and 1920, turned out more than 69,000,000 Muskellunge fry.

The spawning season begins about April 20 and lasts three weeks. The Muskellunge spawns from 100,000 to 300,000 eggs, which are deposited mostly where brush, dead limbs, and logs lie in the water.

Another species of Muskellunge (*Esox immaculatus*) inhabits lakes in northern Wisconsin and Minnesota.

The members of the Pike family are readily distinguished by the scales on cheeks and gill covers. In the Muskellunge the cheek and lower half of gill cover are without scales; in the Pike the cheek is entirely scaled, the lower half of the gill cover being without scales; in the Pickerels cheek and gill cover are both fully scaled.

COMMON WHITEFISH (Coregonus clupeiformis)

(*For illustration see Color Plate XII*)

One of the most abundant and important food-fishes of the North is the Common Whitefish, which inhabits the Great Lakes and some other large lakes of the United States and British America.

There are several species of the genus, mostly of restricted range, inhabiting lakes in the Northwest as far as Alaska, but the Common Whitefish and the Menominee Whitefish (*Coregonus quadrilateralis*), also abundant in the Great Lakes, far exceed the others in commercial value.

The Common Whitefish is in the main the species on which the "Whitefish" industry is based. The catch in 1919 exceeded 6,000,000 pounds, or about half the quantity taken in 1890, so heavy is the drain made upon this food resource. The Whitefish catch along the Canadian shores of the Lakes being equal to that of the United States, we may double the above figures.

The Whitefish fortunately responds readily to artificial methods of propagation, and there are several hatcheries along the Great Lakes devoted to its increase. It is doubtless the favorite food-fish derived from inland waters. Planked Whitefish is considered as great a delicacy in the Lake regions as planked Shad around the shores of the Chesapeake.

The largest part of the catch is made in Lake Michigan and the least part in Lake Ontario. The gill net is the principal apparatus used in capture, but many are taken in pound nets and seines. The Whitefish is seldom taken with the hook, and then only with worm or insect bait.

It inhabits chiefly the deeper parts of the Lakes, moving into shallower waters early in summer, in midsummer seeking again the cooler depths. In the fall months Whitefish again come inshore to spawn, some of them entering streams for that purpose, but the migratory movements vary somewhat in the different Lakes.

Recent investigations have shown that the Common Whitefish is late in maturing, probably not spawning until after five years of age. It deposits on the average about 35,000 eggs, which hatch in about five months.

The food of the Whitefish consists of small crustaceans, small mollusks, and insect larvæ, but chiefly of various kinds of Entomostraca. Whitefish hatched in the Aquarium were carried through the critical period of infancy on a diet consisting of the larvæ of mosquitoes.

These fishes, now ten years old, have lived and grown on a diet of chopped fresh meat. Had it been possible to supply them with their natural live foods, their size would doubtless have been greater. These specimens are apparently the only Whitefishes ever brought to maturity in captivity (see page 131).

Whitefish eggs and young Whitefish are devoured in great numbers by predatory fishes.

The largest Whitefishes seldom reach a weight of 20 pounds, and such are rare, the average as brought to market being only three or four pounds. Females are larger than males.

The Whitefishes as a group are considered the most important fresh-water fishes in the world, and there can be no doubt of the fact that they are undergoing progressive depletion.

FRESH-WATER DRUM (Aplodinotus grunniens)

(*For illustration see Color Plate XIII*)

The Fresh-water Drum is a large fish belonging chiefly to the Great Lakes and the Mississippi Valley. It reaches a length of three or four feet and a weight of 40 or 50 pounds. It is a food-fish, wherever taken, and more popular in the South than in the North.

In 1899 the catch of Drum in the Mississippi and its tributaries exceeded 3,000,000 pounds; in the Great Lakes in 1917 the catch amounted to nearly as much.

The Drum is a bottom fish, living mostly in muddy waters, feeding on Snails, Mussels, and Crayfish, for which its heavy paved teeth are well adapted, and it is not given to the eating of other fishes.

It is not a popular angler's fish, but is often taken with Crayfish bait, and the young are better eating than the adults. The net fisheries take the bulk of those marketed. In the North it is often called Sheepshead, while in Louisiana it is best known as Gaspergou.

The Fresh-water Drum makes drumming or grunting sounds not unlike those made by the Sea Drum, and this is the meaning of its specific name, *grunniens*.

The noises made by Drums, Croakers, and other sound-producing fishes are accomplished by muscles drawn across the air bladder, by the grinding of their blunt teeth, and in other ways, fishes having no real vocal organs.

The ivorylike ear bones, or otoliths, of this fish are popularly known as "lucky-stones," a fancy originating in a marking resembling the letter L.

The Fresh-water Drum has proved to be a hardy fish in the tanks of aquariums, where it gets little of its natural food.

YELLOW PERCH (Perca flavescens)

(*For illustration see Color Plate XIV*)

The Yellow Perch is one of our best-known fresh-water fishes, being abundant throughout the Northern and Eastern States, especially in lakes and ponds. On the Atlantic slope it extends somewhat farther south than in the Mississippi Valley, where it is confined to States bordering on the Great Lakes.

In the North it extends from Nova Scotia and Quebec westward to Minnesota.

The market catch by nets in the Great Lakes sometimes exceeds 9,000,000 pounds a year, while anglers in towns along the Lakes take great numbers and find sport in doing so. The catch by anglers in smaller lakes and ponds everywhere is very large.

The Yellow Perch comes as near to being everybody's fish as any other and but little art is necessary in taking it. It is ready to sample all the baits of the amateur and even responds to baits let down through the ice in winter, when many other fishes are sluggish. The expert takes it both with artificial fly and trolling spoon.

As a food-fish, there is none of better flavor among the commoner kinds. It is easily identified by its broad cross-bands of black, as no other native fresh-water fish wears the same combination of black and gold.

Like other fishes of extended range, it has several names, viz., Yellow Perch, Ringed Perch, Raccoon Perch, Red Perch or Striped Perch, according to locality. Its length may be as much as 14 inches and its weight about three pounds, but such sizes are unusual.

The Yellow Perch is one of the easiest fishes to introduce into new waters. The eggs are extruded in zigzag-shaped bands, which, by the rapid absorption of water, became large masses, seen along the shores in shallow water. Employees of the Aquarium gather such masses in the ponds of Long Island in March and April, which are hatched indoors as a springtime fish-cultural exhibit, the young fry being placed in local streams and ponds.

The egg masses may be found at any time after the ice disappears, according to the latitude.

Yellow Perch have been kept 11 years in captivity on no other food than fish purchased in the markets, although its natural live foods include practically all the smaller forms of fresh-water life.

The Yellow Perch runs in schools and frequents moderate depths. It is a difficult fish to dress because the scales cling so tightly to the flesh.

PIKE-PERCH (Stizostedion vitreum) and SAUGER (Stizostedion canadense)

(*For illustration see Color Plate XV*)

The Pike-perch, perhaps better known as Wall-eyed Pike, ranks next to the Whitefishes and the Lake Trout in quality and commercial importance among the fishes of the Great Lakes, where the market catch in 1917 amounted to 4,500,000 pounds.

While the average weight of this fish in the Great Lakes is less than 10 pounds, it occasionally reaches a weight of 25 pounds and a length of three feet. In other northern waters the average is less than five pounds. The young are usually known as Blue Pike.

Although the Pike-perch inhabits clear waters everywhere in its range, it is a fish of the lakes rather than the rivers. It is found from Lake Champlain westward to Minnesota, in the interior lakes of New York, and in the Mississippi Valley, but through fish-culture operations its habitat has been greatly extended. Its range also extends well into British America.

Perhaps no fish lends itself better to artificial propagation; more than 300,000,000 were liberated from Federal hatcheries on the Great Lakes in 1921. A few millions are hatched annually in the Aquarium, where the process of incubation in glass jars always attracts the attention of visitors. As handled in the fish hatcheries, a large specimen may yield 300,000 eggs.

The Pike-perch belongs to the family of Perches, although its form is suggestive of the Pikes.

While it is regarded in the markets as one of the best of our food-fishes and great numbers are taken in the net fisheries, it is highly appreciated as a game fish. The angler does not find it a difficult fish to catch and a large one will resist like a good-sized Pickerel.

The Sauger, also called Sand Pike, is a little brother to the Pike-perch, resembling it in general appearance, but in size does not average more than a quarter of its weight. It has a smaller eye, a more pointed head, and a lighter coloration. It has much the same geographic distribution.

The Sauger is a good food and game fish, taken in trolling and casting both with bait and lure. In some localities great numbers are taken with seines.

COMMON EEL (Anguilla rostrata)

(*For illustration see Color Plate XVI*)

The annual catch of Eels for market along the Atlantic coast from Maine to Florida exceeds 3,000,000 pounds and is worth $250,000.

Recently three barges, each more than 100 feet long and 12 feet wide, arrived at New York from Quebec with 165,000 pounds of live Eels. They were towed by way of the St. Lawrence River, Lake Champlain, and Hudson River and were 13 days in transit. The barges are virtually well-boats, or live cars, the bottoms consisting of heavy slats, with narrow spaces between to provide abundant circulation of water.

The catch is made when Eels are working toward salt water and is heaviest during the dark of the moon. The season is from July to October, inclusive.

Large as is the catch of Eels in America, it is vastly more so in Europe.

Science knows more to-day about the Eel than it did some years ago, and the missing chapters in the Eel's life history have been supplied through modern deep-sea investigations rather than in the study of fresh or coastal waters, where Eels are more in evidence.

Unlike Salmon, Shad, and other fishes which enter fresh waters to spawn, the Eel descends streams at maturity to spawn far at sea. The young Eels—three inches or so in length, called Elvers—that enter fresh waters in the spring in large numbers, and are continually working upstream, have always been known, but the stages of growth between the egg and the Elver were not.

These stages in which the baby Eel does not exceed three inches in length are of comparatively recent discovery. We here find it a thin, flattened creature, so transparent that ordinary print may be clearly read through its body. When first described in this stage it was called *Leptocephalus* and was not known to be the Common Eel.

These transparent larval Eels found at sea in the winter months grow rapidly, and by the end of the year are more than two inches long, when they begin to transform. By the time they are a year old they begin to appear in fresh-water streams as Elvers or young Eels about three inches long.

Investigations by the Danish vessel *Dana* in 1920 and 1921 have shown that the early larval stages of both the American and the European Eel are found only in the western Atlantic, at depths of 600 to 900 feet. The former spawns to the south and southwest of the Bermuda Islands, the latter to the south and southeast.

While the American Eel begins to enter fresh water at the age of a year, the European species remains three years in the larval stages before it appears as the Elver in European streams. The latter, like the American Eel, goes far inland, even passing within the borders of Switzerland.

Females with ripe eggs are unknown, the millions of undeveloped eggs carried by each female not developing while the Eels linger in fresh or coastal waters.

The Eels found far inland are always females and remain in fresh water for several years. It is only when tending toward reproductive maturity that they seek the sea. Male Eels remain in tidal waters and are smaller and less in evidence. Like females, they do not reach breeding maturity until they have passed to sea.

The great bulk of the Eel catch everywhere consists of females. It is said that all the Eels captured in the great Quebec fishery are females moving downstream.

The Eel catch in the St. Lawrence River is derived from Eels belonging to that river and its tributaries, including Lake Ontario. The Lake Ontario catch of Eels in 1899 exceeded 123,000 pounds. The annual yield of all the other Great Lakes combined seldom exceeds 2,000 pounds, the Falls of Niagara constituting an impassable barrier to all kinds of fishes.

Enormous numbers of young Eels gather below Niagara in spring and summer, but there is no evidence that they ever pass farther by that route.

The Eels of the upper Lakes may pass up by way of the Erie and Welland canals. It may be that limited numbers of Eels in the Mississippi River find means of passing into the Great Lakes. Whether Eels inhabited these lakes before the construction of canals, the writer is not informed. The fishery statistics at hand contain no records of Eels in Lake Superior.

Eels enter all American streams from the St. Lawrence River to the Gulf of Mexico. It is only the young Eels that move upstream. Adults move downstream and do not return. Both males and females die at sea after the first and only breeding season in their lives. The Eel is very prolific, each female producing from 5,000,000 to 10,000,000 eggs.

Eels are taken in other ways than with nets. "Bobbing for Eels" is done with worms strung on thread, which looped in a small bunch make a bait very attractive to Eels. They are also taken in small wire traps called eelpots, by eel-spears, and are even taken by digging and spearing in the mud, where they bury themselves in winter.

AMONG THE SKYSCRAPERS OF A HERON VILLAGE

A nearly-grown young bird in the foreground left the nest when the camera man sat down in it. This colony of Great Blue Herons is in a big sycamore grove at the southern end of San Francisco Bay.

JOURNAL of the PAN-PACIFIC RESEARCH INSTITUTION

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Address all communications to MID-PACIFIC MAGAZINE, 1067 Alakea St., Honolulu, Hawaii, for attention of THE EDITORS. An open forum for discussion of problems concerning food production, distribution, conservation and consumption; public health; current habits and customs, or any subject relative to human welfare in countries bordering upon the Pacific Ocean.

Fishes of the American Northwest

A Catalogue of the Fishes of Washington and Oregon, With Distributional Records and a Bibliography

By Leonard P. Schultz and Allan C. DeLacy

School of Fisheries, University of Washington, Seattle, U. S. A.

INTRODUCTION

THIS CATALOGUE is divided into the following five parts, which are: I. Catalogue of the fishes of Washington and Oregon with distributional records. II. A list of species whose occurrence in Washington and Oregon is doubtful. III. Bibliography. IV. Index to scientific names of fishes. V. Index to common names of fishes. VI. Index to geographical locations. The catalogue includes those species of fish known to occur in Washington and Oregon, either from published records or from specimens collected by Carl L. Hubbs and Leonard P. Schultz in 1926, the senior author, and many of his students since 1928. Those most active in collecting fishes have been, Howard Baltzo, Wilbert Chapman, Allan C. DeLacy, Leo Erkkila, Claude Flock, George Garlick, Samuel Hutchinson, Tom Martin, Daniel Merriman, Loyd A. Royal, Ralph Silliman, Richard T. Smith, William A. Spoor, Lawrence Townsend, Arthur D. Welander, Rennie Wells, and Albert Young.

In general, economic fisheries papers and papers of a popular nature have not been included in the bibliography unless they contain definite authentic identifications with scientific names of species and distributional records. Common names, except where they specifically refer to a particular species, have not been used in compiling this paper.

The punctuation used in this catalogue has a definite meaning. For example see species number 37. Following the number "37" are the numbers "(779a, 779c, 779h)" in parenthesis, which refer to the number of this same species in the publication by Jordan and Evermann (1896-1900). Below the name *Salmo clarkii clarkii* is given in small type the specific name used in the original description by the author, and a reference to his paper including the type locality. Following the type locality "Cathlopootl R., Oregon" is a colon, and then the names of the authors who did not describe this particular species are listed after the colon. These authors merely used that scientific name in their publications. Likewise, in the list of synonyms in the next paragraph below, a colon separates the scientific name and its author or describer (if his name is in the list of authors who furnished records) from those authors who merely made use of the name in their publications. For example "*Salmo brevicauda* Suckley 1862a: 1874; Günther 1866".

Washington and Oregon have been divided into certain geographical regions arranged as follows: Puget Sound Region, or Puget Sound Drainage; Coast of Washington; Columbia River Mouth; Columbia River Drainage; Coast of Oregon; Oregon Lakes

STATE OF CALIFORNIA—RESOURCES AGENCY

EDMUND G. BROWN JR., Governor

DEPARTMENT OF FISH AND GAME
1416 NINTH STREET
SACRAMENTO, CALIFORNIA 95814
(916) 445-5186

July 28, 1980

Dear Colleague:

We enclose a copy of the final draft of our revised list of the freshwater and anadromous fishes of California. We do not expect you to wade through the entire manuscript, but would greatly value your comments and suggestions regarding those sections of interest to you.

We are sending copies of the manuscript to a number of individuals well informed regarding some or all of the fishes listed.

We hope to have the manuscript to the printer during the first week in September.

Sincerely,

Leo

Leo Shapovalov
Senior Fishery Biologist (retired)

Almo

Almo J. Cordone
Senior Fishery Biologist

Bill

William A. Dill
Senior Fishery Biologist (retired)

AJC:cm

Enc.

DRAFT-7-24-80

LIST OF THE FRESHWATER AND ANADROMOUS FISHES OF CALIFORNIA[1]

Leo Shapovalov[2], Almo J. Cordone, and William A. Dill[2]

Inland Fisheries Branch

California Department of Fish and Game

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1/ Accepted for publication________________________.

2/ Retired.

ABSTRACT

This list is the second revision of the checklist first published by Shapovalov and Dill (1950). The first revision was authored by Shapovalov, Dill, and Cordone (1959). The present list consists of a main list of native and established exotic freshwater, anadromous, and euryhaline species, supplementary lists of native species extinct or extirpated from California, and exotic species unsuccessfully introduced or of uncertain status, plus lists of marine fishes successfully introduced into the Salton Sea and forms and names new to the main list since 1959.

INTRODUCTION

Two previous editions of this list have been published (Shapovalov and Dill 1950; Shapovalov, Dill, and Cordone 1959). Since publication of the 1959 list, many changes have occurred in both the composition of the fauna and the nomenclature applied to many of the fishes.

First, a number of introductions have been made into the State. Some of these fishes have been introduced by the California Department of Fish and Game as part of its research and management program. Others have been introduced illegally, either deliberately or inadvertently, especially by aquarists and tropical fish farmers. At the same time, some forms have become extinct or have been extirpated from State waters.

Second, some new forms have been described and the nomenclatural status of a number of others has been revised by systematists. Some of the revisions have been in the direction of condensation, simplification, and uniformization of group names, while others have been in the opposite direction of ever greater diversification. With full recognition that opinions on nomenclature may differ decidedly, we have attempted to include in the list all revisions that have been proposed by recognized systematists in scientific publications and not subsequently refuted.

The list itself is preceded by several introductory sections. Those entitled "Scientific Names" and "Common or Vernacular Names", which are of a background nature, are printed here with little change from our previous list.

ACKNOWLEDGMENTS

We are indebted to the following individuals for their cooperation and genuine interest: Reeve M. Bailey, Lillian J. Dempster, W. I. Follett, the late Carl L. Hubbs, Robert N. Lea, Robert R. Miller, and Peter B. Moyle. We appreciate the criticism by these scientists and have incorporated many of their suggestions in the final list. We have not, however, been able to reconcile all our differences, so one should not assume that these scientists are in complete agreement with all of the names listed here.

PURPOSE

Two major objectives in publishing a checklist of California freshwater and anadromous fishes were cited in the 1950 edition and reiterated in the first revision (1959). These were to: (i) establish the basis for compilation of a detailed handbook of these fishes, and (ii) promote stability and uniformity in both their common and scientific names. Publication of a key to these species by Kimsey and Fisk (1960) and especially, publication of "Inland Fishes of California" by Moyle (1976), have aided in achievement of the first goal. The second objective has neared achievement with regard to common or vernacular names. However, uniformity of nomenclature of scientific names appears to continue as a never to be completed goal.

This list, like the previous ones, will of course become obsolete in time, and another edition will be necessary. We suggest that its future authors, or any who propose to publish local, state, or nationwide lists, can materially advance stability in fish nomenclature by attempting to resolve differences through consultation with the various experts in the field who have authored existing lists. We have consistently done this, have invariably met with cooperation, and thereby have resolved most problems.

SCIENTIFIC NAMES

In scientific naming, stability is largely dependent upon the thoroughness and care of the taxonomist. Any proposed revisions must be carefully evaluated. For example, Schultz (1957:48-49) stated:

"The evaluation of generic characters and recognition of genera is possible only when a comprehensive study is made of a family on a worldwide basis and when there is established the nature of the similarities and differences among groups of species...

"The problem of how far to progress nomenclatorially in recognizing generic categories must be resolved in a practical manner so that biologists are not presented with a confusion of ill-defined genera. Usually this confusion and lack of agreement among ichthyologists and fishery biologists result from inadequate studies of a family. Obviously, no dependable solution is possible on how many genera and subgenera to recognize in a family until the zoological relationships of all its species have been adequately compared morphologically, physiologically, and as to habits. No doubt, after this work has been done, a middle-of-the-road or even a conservative attitude on the number of phyletic lines to name would meet with general acceptance. Too often in ichthyology there is a tendency either to unite genera without adequate study or to establish new genera without any attempt to review the family. The least confusion results if the present status of each genus in a family is retained until such time as it is thoroughly studied."

We are in accord with this opinion but believe that the ideas expressed are applicable to species and subspecies as well. Subspecies in particular are subject to much lumping and partitioning, at times without secure evidence. Some ichthyologists have seriously questioned the existence of certain forms on our list while, on the other hand, they have proposed hitherto unknown forms for inclusion. In almost every case, we have let the decision hinge on the appearance of substantiating data in the literature. The publication of new scientific names and elimination of familiar ones without sufficient supporting evidence accomplishes little and furthers confusion in fish nomenclature.

Bailey (1956:328-329) has given considerable thought to the problem of subspecies: "...the common taxonomic practice of dividing geographically variable species into named races, or subspecies, has been subjected to critical scrutiny. It has been noted that the pattern of geographic variation in some species takes the form of a rather gradual and progressive gradient, termed a cline. It is now agreed by many taxonomists that despite the high biological significance of this type of variation it is undesirable to assign subspecific names on the basis of clinal gradients...

"Commonly the differences between geographic subspecies are slight and are best expressed as average conditions applying to a considerable fraction of individuals, but not to all. It is my revised opinion that acceptable subspecies should evidence high uniformity over the respective ranges and should differ one from another with high constancy. Zones of intergradation should be rather narrow. If they are wide the variation merges insensibly into a clinal gradient...

"The ichthyologist, in studying material, often perceives differences among populations from various parts of the geographic range of a species. Such discoveries may presage the definition of validly recognizable subspecies. The premature use of such information without publication of the full data is disconcerting to other workers, who are unable to evaluate the basis for the action. The different stocks sometimes turn out to be fully distinct species..."

Another excellent discussion of the subject which supplements the above statements was presented by Bailey, Winn, and Smith (1954:148-150). The following excerpt seems particularly pertinent:

"Many clinal variations in the morphology of fishes may be caused partly or wholly by gradients of environmental factors, especially temperature. The assumption that all taxonomic characters, such as meristic counts, are governed solely by genetic factors is no longer tenable... Whether the gradient is caused by heredity or the environment, we reject the practice of establishing subspecies on characters that show clinal variation. Furthermore, the insistence that a cline be a perfectly smooth gradient, we regard only as an academic problem. Minor irregularities are to be anticipated because of local genetic emphasis, sampling errors, environmental variations that impose structural change, and other vagaries."

We concur in the statements above and in keeping with them have employed binomials instead of trinomials wherever sufficient published evidence exists to show that a cline truly exists. This has been done, for example, for Notemigonus crysoleucas (Bailey et al. 1954: 123-124, 149; Hart 1952:33-38, 77); and Ictalurus punctatus (Bailey et al. 1954:

130). Subspecific partitioning of many species in the main list may be of questionable validity; however, we retain the status quo and await the publication of evidence showing whether or not the trinomials are justified.

Space does not permit a description of each change in scientific names used in bringing this list up to date, although many such changes are described. Most of the major changes are discussed in appropriate text sections that follow. Recourse to the references will provide further details. Some of the more important relatively recent references include: Bailey and Bond (1963), Bailey and Uyeno (1964), Bond (1961), Hopkirk (1973), Hubbs (1967), Hubbs, Follett, and Dempster (1979), Kliukanov (1970), Miller (1958), Moyle (1976), Rosen and Bailey (1963), Ross (1973), Smith (1966), and Walker, Whitney, and Barlow (1961).

COMMON NAMES

Stability in common naming can best be achieved by adhering as closely as possible to a workable set of criteria, as outlined below.

The selection of common names for California freshwater fishes is complicated by two somewhat paradoxical factors: the multiplicity of names which have already been applied to certain species and, in the case of certain other forms, the dearth of common names. Thus, members of the genus *Cyprinodon* have been called by such varied names as desert minnow, desert killifish, pursy minnow, pygmy fish, and pupfish. Conversely, a large number of native cyprinids are so similar and indistinctive in appearance that the layman has never recognized their specific differences nor called them by any name other than the rather general chub or shiner. This list attempts to reconcile such difficulties by assigning one official common name to each species and subspecies.

The basic rules or criteria for the selection of common names remain identical with those presented in the previous lists. The principles again have proven of practical value in the objective establishment of the revised common names. Such guides are necessary to prevent arbitrary selection based on personal preference. Insofar as possible, we have adhered to them, as follows:

1. Names should agree with those in actual common use; or when there is no common or vernacular use, with those in published literature. Strictly "book names" should be avoided.
2. Names should agree, if possible, with those on other authoritative lists, especially those of the Committee on Names of Fishes of the American Fisheries Society (Robins et al. 1980) and Hubbs et al. (1979).
3. Names should indicate relationship and not confuse it.
4. Names should be descriptive.
5. Preference should be given to names which are short, distinctive, interesting, catchy, romantic, or euphonious.

Each of these qualifications has exceptions which makes it useless by itself. Therefore, each principle listed above should be read as though it were prefaced by the words, "Other considerations being equal..." For example, the name Sacramento perch does not meet either Rule 3 or 4 above, since this species (Archoplites interruptus) is not a true perch. However, since it is so commonly used (Rule 1) and since it agrees fully with the name used in the lists cited in Rule 2, it would be foolish to select another name.

Aside from such considerations, in this revision, as in the previous one, we have attempted continued advancement of the twin ideals of stability for individual names and the designation of relationships through the selection of common names according to a definite plan. Such aims have long been recognized by ornithologists and are well exemplified by the names listed in "The Distribution of the Birds of California" (Grinnell and Miller 1944). Thus, wherever possible the same basic common name has been given to all members of a single genus, with prefixes added to that common name for each full species of that genus. In the case of subspecies, additional prefixes have been added to the specific name. For example, all members of the genus *Gila* have been termed chub, members of the *Gila bicolor* group have been termed tui chub; and each subspecies of the group is further designated by an additional term such as Mohave for *G. b. mohavensis*, the Mohave tui chub.

It should be noted that this method will permit the retention of at least part of the common name even if the species or subspecies undergoes a revision which will change the scientific name. This, in part, answers the criticism of the Committee on Names of Fishes of the American Fisheries Society (Robins et al. 1980), "The practice of applying a name to each genus, a modifying name for each species, and still another modifier for each subspecies, while appealing in its simplicity, has the defect of inflexibility." Further, "If a fish is transferred from genus to genus, or shifted from species to subspecies or vice versa, the common name should nevertheless remain unaffected. It is not a primary function of common names to indicate relationship."

We contend that to reveal, rather than confuse, relationships should be an important and vital function of common names. Some of the most deeply-rooted vernaculars are completely misleading; little can be done now to establish meaningful names. When a name is entered in an official list it should not be changed unless there are important reasons for it. However, changing the name to maintain the proper relationship of a form known to professional fisheries people but unfamiliar to laymen does not present a serious problem and to us is justifiable. In any event, preparation of this present revision showed that the system was workable and had meaning, with no major difficulties encountered.

The authors are inclined to share the opinion of Robins et al. (1980) and Alden H. Miller (Grinnell and Miller 1944) that only full species deserve common names. Nevertheless, we have listed common names for each subspecies, with full recognition that a number of them may not endure. One reason prompting this decision is that certain subspecies have been distinguished as entities almost from the beginning, and it would seem unfortunate to obscure (through omission) such names as kokanee and Paiute.

It should also be noted that a number of systematists have disagreed with certain of our groupings; e.g., that for the native trouts, in which assignment to specific or subspecific status is, in some instances, original with the authors. However, a firm nomenclature has never been developed for some of these plastic groups. And, as we have stated before, even after some decided changes in scientific nomenclature, most of our common names can still be retained with enough recognizable parts to promote stability.

SCOPE

The main list covers both native and successfully established exotic species. The supplementary list includes exotic species unsuccessfully introduced or of uncertain occurrence.

We have attempted to include all native forms whose occurrence has been reported and not disproved in the literature or verified through the examination of collections. The existence of some of these as valid species or subspecies (*Catostomus occidentalis lacusanserinus*, for example) has been questioned by some workers. Our criterion for inclusion of such forms is very simple: we have tried to include all forms whose taxonomic identity has not yet been disproved in published literature.

Possibly certain other records of occurrence are based on misidentification. Possibly some of the native species are no longer a part of our fauna. Native forms which are now either extinct or extirpated from State waters include *Salvelinus malma*, *S. confluentus*, *Gila crassicauda*, *Gila elegans*, *Pogonichthys ciscoides*, *Ptychocheilus lucius*, *Cyprinodon macularius californiensis*, *C. nevadensis calidae*, and *C. n. shoshone*. However, it is practically impossible to prove or disprove such suppositions. Hence, in the case of the native species it has been thought best to err on the side of inclusiveness rather than on the side of exclusion. On the other hand, only those exotic or introduced species of which breeding populations are known to have survived are included in our main list.

Fishes recorded only from outside California have not been included if the stream in question flows into or out of this State, e.g., the Klamath and Truckee rivers. However, in the case of the

Colorado River, which is a boundary stream, fishes recorded from the Arizona side of the stream have been included.

Hybrids have also been omitted. Both interspecific and intergeneric hybrids of a number of the species listed have been recorded from the natural waters of California (e.g., Hubbs and Miller 1943).

Marine Fishes Successfully Introduced into the Salton Sea

Most of the fishes in the checklist are strictly freshwater or anadromous. For the sake of completeness we have also listed those marine and brackishwater species which are known to penetrate into fresh water. However, strictly marine species from the Gulf of California which have been introduced into and have successfully spawned in the Salton Sea, an inland body of water with salinity approaching that of ocean water, are omitted from the main list. They are included below, since they have established breeding populations in an inland body of water. The story of these introductions has been told by Anon. (1958) and Walker et al. (1961).

Four species presented in the main list are also firmly established in the Sea: *Poecilia latipinna*, *Tilapia mossambica*, *Gambusia affinis affinis*, and *Gillichthys mirabilis* (G. F. Black, Fishery Biologist, Calif. Dep. Fish and Game, pers. commun.). *Dorosoma petenense* and *Tilapia zillii* are common in the Sea but apparently spawn only in drains entering the Sea. *Mugil cephalus* and *Cynoscion parvipinnis* were formerly present but have not been observed for a number of years. The formerly abundant *Cyprinodon macularius* has been drastically reduced in recent years, with only an occasional specimen now showing up in the shallow margins of the Sea (Black 1980).

HAEMULIDAE—grunt family

Anisotremus davidsonii (Steindachner)—sargo

Introduced in 1951. The first sargo known to have been spawned in the Sea, a juvenile young-of-the-year, was taken in October 1956. The first verified catch of an adult was made on 17 September 1958. Since then sargo up to 305 mm (12 in.) in length have been taken by sport fishermen in considerable numbers.

SCIAENIDAE—croaker family

Bairdiella icistia (Jordan and Gilbert)—bairdiella

First introduced in October 1950. The population of bairdiella is now very large. They are firmly established and should remain unless the salinity of the Sea becomes too high to support fish life.

Cynoscion xanthulus Jordan and Gilbert—orangemouth corvina

First introduced in October 1950. They are now present in large numbers.

Forms and Names New to the Main List Since 1959

Numerous changes in scientific and common names have taken place since the 1959 checklist was prepared. Changes involving common names and those minor revisions in scientific naming are not explained. A total of 61 forms and names not listed in the 1959 checklist has been added to this revised edition. They are repeated here with a brief explanation and documentation as evidence for their inclusion. Included are 12 newly described species and 18 newly recognized subspecies. Five subspecies and 14 species of exotic fishes have become established in California waters since 1959.

Although the California freshwater fish fauna has been studied for many years, some undiscovered species may remain. Collecting in coastal fresh waters may uncover additional euryhaline forms. Taxonomists may be expected to continue to describe new forms but at a lesser rate than in the past. For example, some taxonomists have recognized a trout from northern California as a distinct species and have proposed the common name of redband trout, but have not yet given it a scientific name. The escape or release of tropical fish into the wild may be anticipated and some of these may become established.

Although such activities have a much lower priority now than in the past, the introduction of exotic game and forage fishes by the California Department of Fish and Game may provide new species. The fish management program of the Inland Fisheries Branch includes as part of its long-range planning an evaluation of the various aquatic habitats and what might constitute the most suitable game and/or forage species, either native or exotic. Each potential import is thoroughly studied and screened to insure against detriment to existing fisheries.

PETROMYZONTIDAE—lamprey family

Lampetra folletti (Vladykov and Kott)—Modoc brook lamprey

Vladykov and Kott (1976*b*) described this nonparasitic species of lamprey from the Klamath River system in Modoc County, California, as *Entosphenus folletti*. We follow Hubbs (1971) in treating *Entosphenus* as a subgenus of *Lampetra*.

Lampetra hubbsi (Vladykov and Kott)—Kern brook lamprey

Valdykov and Kott (1976*a*) described this nonparasitic species of lamprey from the Friant-Kern Canal, east of Delano, San Joaquin Valley, as *Entosphenus hubbsi*. We follow Hubbs (1971) in treating *Entosphenus* as a subgenus of *Lampetra*.

Lampetra lethophaga Hubbs—Pit-Klamath brook lamprey

The addition of this species is based on its description by Hubbs (1971). It is found in the drainage basin of the Pit River (a Sacramento River headwater) in northeastern California, and in the upper Klamath River in south-central Oregon. In the past it has been misidentified as Lampetra planeri and Entosphenus tridentatus.

Lampetra pacifica Vladykov—Pacific brook lamprey

This small, nonparasitic lamprey was described as a new species by Vladykov (1973). In California, it is recorded from various streams in the Sacramento-San Joaquin River system. It is quite similar to L. richardsoni and may not be specifically distinct from it. Before 1973 it had frequently been referred to L. planeri or L. richardsoni.

Lampetra richardsoni Vladykov and Follett—western brook lamprey

Vladykov and Follett (1965) described this new nonparasitic species of lamprey from "streams of British Columbia, Washington, Oregon, and possibly Alaska." Follett subsequently informed J. D. Hopkirk (pers. commun.) that the range of the western brook lamprey was more recently known to include California. Various authors had previously listed it as L. planeri, the name used in our 1959 check list. However, L. planeri is the European brook lamprey.

Lampetra tridentata (Gairdner)—Pacific lamprey

Originally listed as Entosphenus tridentatus in our 1950 and 1959 checklists, we follow Hubbs (1971) in treating Entosphenus as a subgenus of Lampetra.

ACIPENSERIDAE—sturgeon family

Acipenser medirostris medirostris Ayres—American green sturgeon

We follow Lindberg and Legeza (1965:33) in recognizing this subspecies. In our 1959 checklist we listed only the full species, *Acipenser medirostris* Ayres.

CLUPEIDAE—herring family

Clupea harengus pallasii Valenciennes—Pacific herring

In our 1959 list the Pacific herring was listed as *Clupea pallasii*. However, Svetovidov (1952) has shown that this form is actually a subspecies of *C. harengus*.

OSMERIDAE—smelt family

Hypomesus nipponensis McAllister—freshwater smelt

This species was introduced into California (our shipment of eggs) in 1959 (Wales 1962). At the time it was misidentified as *H. olidus*. This strictly freshwater species has since become firmly established in at least several waters in California.

Hypomesus transpacificus McAllister—delta smelt

In his revision of the smelt family, McAllister (1963) described this new species, known only from the lower parts of the Sacramento and San Joaquin rivers. It had previously been referred to in the literature as *Hypomesus olidus*, the name we used in our 1959 checklist.

McAllister described two subspecies, *H. transpacificus transpacificus* and *H. transpacificus nipponensis*. However, we follow Kliukanov (1970) in treating the two as distinct species.

COREGONIDAE—whitefish family

Prosopium williamsoni (Girard)—mountain whitefish

Our 1959 list placed this species in the genus *Coregonus*. We follow

Norden (1961) who described the characters separating the two genera.

SALMONIDAE—salmon and trout family

Salmo clarkii pleuriticus Cope—Colorado River cutthroat trout

This subspecies was dropped from the main list in our 1959 checklist because published reports of its occurrence in the Salton Sea region were old and somewhat dubious. The reported specimens may have been misidentified; in any case, they almost certainly consisted of specimens washed into the basin from the Colorado River many years ago. No specimens were known to exist in any collections.

On 11 September 1974, the California Department of Fish and Game collected 21 specimens of this subspecies from the lower three of the five Williamson lakes of the southern Sierra Nevada. These trout were descendant from eggs of Colorado River cutthroat trout taken in 1931 from Trapper's Lake, Colorado (Gold, Gall, and Nicola 1978).

Salvelinus confluentus (Suckley)—bull trout

Although the view that the Dolly Varden, *Salvelinus malma*, is the only recognizable member of the genus in the American northwest has been widely accepted, the subject has been a matter of some controversy for over a century. Morton (1970) concluded that *S. malma* was the only valid species and that there were no valid subspecies. More recently, Cavender (1978) presented morphometric, meristic, osteological, and distributional evidence to support his view that there are two widely distributed forms of *Salvelinus* native to the western United States and Canada: the Dolly Varden, *S. malma*, and the bull trout, *S. confluentus*. He records both species from the McCloud River drainage in California, although his only record of *S. malma* consists of two specimens in the U. S. National Museum labeled as having been sent by Livingston Stone from the McCloud River in 1877. To us, it seems virtually inconceivable that both species could have coexisted within the restricted confines of the McCloud River.

CYPRINIDAE—carp or minnow family

Gila bicolor (Girard)—tui chub

Bailey and Uyeno (1964) changed the name of this species from Siphateles bicolor, the name used in the 1959 checklist, to Gila bicolor.

Gila bicolor mohavensis (Snyder)—Mohave tui chub

For many years this fish had been accorded full species rank, but Miller (1973) regarded it as a subspecies, because he was unable to discover characters that would separate it specifically from all populations of Gila bicolor in the Lahontan Basin.

Gila bicolor snyderi Miller—Owens tui chub

This subspecies was described by Miller (1973). In our previous checklist it was listed as Siphateles bicolor obesus. It is confined to the isolated Owens Valley in eastern California.

Gila bicolor thalassina (Cope)—Goose Lake tui chub

This subspecies was not included in the 1950 and 1959 checklists because of the belief that it was extinct in Goose Lake, Modoc County (Hubbs and Miller 1948:70-71). A prolonged drought period (1929-1934), when Goose Lake was virtually dry, may have led Hubbs and Miller to this conclusion. Recent collections made by T. J. Mills (Fishery Biologist, Calif. Dep. Fish and Game, pers. commun.) revealed that this chub is once again very abundant in Goose Lake. Its identity as G. b. thalassima was confirmed by C. E. Bond (15 August 1978 letter to T. J. Mills).

Gila bicolor vaccaceps Bills and Bond—Cowhead Lake tui chub

Tui chubs from Cowhead Lake, Modoc County, were first recognized as distinct by Hubbs and Miller (1948) and ultimately described by Bills and Bond (1980). The lake is now dry and the chubs are confined to the small outlet slough.

Gila coerulea (Girard)—blue chub

This species, from the Klamath River system, was listed in our 1959 checklist as *Gila bicolor*. Bailey and Uyeno (1964) have explained why it should be called *G. coerulea*.

Gila elegans Baird and Girard—bonytail chub

In our 1959 checklist we used the name *Gila robusta*, and treated the form from the Colorado River as a subspecies, *G. robusta elegans*. *G. robusta elegans* is regarded as having specific status by Minckley and Deacon (1968).

Hesperoleucus symmetricus mitrulus Snyder—Upper Pit western roach

Hesperoleucus symmetricus navarroensis Snyder—Navarro western roach

Hesperoleucus symmetricus parvipinnis Snyder—Gualala western roach

Hesperoleucus symmetricus venustus Snyder—Venus western roach

In our 1959 checklist these subspecies were accorded full specific rank. We now concur with Moyle (1976:180) and Hubbs et al. (1979) that they should be treated as subspecies of *H. symmetricus*. Hopkirk (1973: 48-51) describes some of the taxonomic problems involved and the need for a thorough revision of the genus.

Lavinia exilicauda chi Hopkirk—Clear Lake hitch

Hopkirk (1973) described this subspecies from Clear Lake in central California, separating it from *Lavinia exilicauda exilicauda* of previous authors. He remarked that it "is a lake-adapted subspecies with a high number of gill rakers. In this respect, it agrees with Pogonichthys ciscoides and Hysterocarpus traskii lagunae from Clear Lake basin".

Pogonichthys ciscoides Hopkirk—Clear Lake splittail

Hopkirk (1973) described this species from Clear Lake in central California, distinguishing it from Pogonichthys macrolepidotus of previous authors. He noted that it "is a lake-adapted species with fine gill rakers, terete body, terminal mouth, and small fins."

CATOSTOMIDAE—sucker family

Catostomus fumeiventris Miller—Owens sucker

This species was described by Miller (1973). For some years it had been recorded as Catostomus arenarius. It was originally confined to the isolated Owens Valley in eastern California, but has been introduced into June Lake in the Mono Lake Basin, and possibly into the Santa Clara River Basin by way of the Los Angeles Aqueduct.

Catostomus luxatus (Cope)—Lost River sucker

We follow Hubbs et al. (1979) in placing the species listed in our 1959 edition as Deltistes luxatus in the genus Catostomus.

Catostomus occidentalis humboldtianus Snyder—Humboldt western sucker

Catostomus occidentalis mniotiltus Snyder—Monterey western sucker

These subspecies were treated as full species in our 1959 list. They are currently recognized as subspecies of Catostomus occidentalis (Hopkirk 1973:69; Moyle 1976:214; Hubbs et al. 1979).

Catostomus platyrhynchus (Cope)—mountain sucker

In our 1959 checklist we listed Pantosteus lahontan, Lahontan mountain sucker. Smith (1966) united Pantosteus platyrhynchus and P. lahontan as Catostomus platyrhynchus.

Catostomus santaanae (Snyder)—Santa Ana sucker

In our 1959 checklist this species was listed as Pantosteus santaanae Snyder. Smith (1966) relegated Pantosteus to a subgenus of Catostomus.

COBITIDAE—loach family

Misgurnus anguillicaudatus (Cantor)—Oriental weatherfish

On 12 April 1968, J. A. St. Amant collected loaches in a portion of the Westminster flood control channel, Orange County (St. Amant and Hoover 1969). They were identified as Misgurnus anguillicaudatus by C. L. Hubbs. This was the first verified record of free-living loaches in California. The source of the loaches is believed to be the Pacific Goldfish Farm, from which some loaches escaped into the channel as early as the 1930's. A thriving population was present upstream from the original collection site in 1977 and another population was discovered in the adjacent Bolsa Chica Channel in 1979 (F. G. Hoover, Fishery Biologist, Calif. Dep. Fish and Game, pers. commun.).

ICTALURIDAE—North American freshwater catfish family

Ictalurus furcatus (Lesueur)—blue catfish

The blue catfish is presently established in four reservoirs and several ponds in San Diego and Riverside counties and several ponds at the Imperial Wildlife Area in Imperial County. The initial plant of blue catfish in California was made by the California Department of Fish and Game in October 1966 when 1,758 fish from Stuttgart, Arkansas, were released in Lake Jennings, San Diego County (Richardson et al. 1970). A single 1.7 kg (3.7 lb) specimen was collected from the San Joaquin River near Mossdale

San Joaquin County, in December 1978 by the Department's Bay-Delta Study (Taylor 1980). Currently about 20 commercial fish farmers in California are licensed to rear and sell this species.

Pylodictis olivaris (Rafinesque)—flathead catfish

A collection of four young-of-the-year specimens from the Highline Canal and its tributaries, near Niland, Imperial County, constituted the first California record for this species (Bottroff, St. Amant, and Parker 1969). They were probably progeny from the original introduction by the Arizona Game and Fish Department of 600 fish into the Colorado River above Imperial Dam. The flathead is now common in the Colorado River and adjacent waters from Imperial Dam upstream to Headgate Rock Dam near the town of Parker. It is also common in the All American Canal system, including the various drains and canals in Imperial Valley.

CYPRINODONTIDAE—killifish family

Cyprinodon macularius macularius Baird and Girard—Colorado Basin desert pupfish

Cyprinodon macularius californiensis Girard—San Diego desert pupfish

The 1950 and 1959 checklists did not include these subspecies. R. R. Miller advised W. I. Follett (pers. commun.) that Girard's (1860) original description of Cyprinodon californiensis, collected in the neighborhood of San Diego, is actually a subspecies of the desert pupfish. Hubbs et al. (1979) include it in their list.

Cyprinodon milleri LaBounty and Deacon—Cottonball Marsh pupfish

LaBounty and Deacon (1972) described this pupfish from Cottonball Marsh, located in an isolated sector of the northwest portion of

Death Valley. Previously these pupfish had been considered as a population of C. salinus.

Lucania parva (Baird)—rainwater killifish

Hubbs and Miller (1965) describe the establishment of this cyprinodont in Irving Lake, Orange County, and streams and sloughs tributary to San Francisco Bay. Relatively few specimens (three in November 1963 and six in June 1964) were taken from Irving Lake and the status of this population is unknown. However, concerning the Bay, the authors state, "It is obvious that Lucania parva has become well established about San Francisco Bay and contiguous waters, with vast increase in numbers and in range." These populations were first noted in the late 1950's. Another population was discovered in 1976 in Arroyo Seco Creek, a tributary of Vail Lake, Riverside County (McCoid and St. Amant 1980).

POECILIIDAE—livebearer family

Poecilia latipinna (Lesueur)—sailfin molly

In our 1959 checklist we listed Mollienesia latipinna. Mollienesia was synonymized with Poecilia by Rosen and Bailey (1963). It should also be noted that the 1959 report mentioned that this species was established in canals and ditches tributary to the Salton Sea. Now it is by far the most abundant species in these habitats, as well as in the shallow margins of the Sea itself (Black 1980).

Poecilia mexicana mexicana Steindachner—Orizaba shortfin molly

The Orizaba shortfin molly has been established in the Salton Sea area for many years. It was first reported in 1964 from a small pond and its tributary about 8 km (5 miles) north of the Salton Sea (St. Amant 1966). Further collections were made in this general area in subsequent years.

Populations of shortfin mollies have persisted in scattered locations in the drains and natural water courses entering the Salton Sea and in the margins of the Sea itself (Black 1980). They are much less abundant and widespread than the sailfin molly, Poecilia latipinna, but nevertheless can be considered a permanent member of the fish fauna in these waters.

St. Amant and Hoover (1969) noted their occurrence (misidentified as Poecilia sphenops) in a coastal flood control channel in Orange County, the only report from outside the Salton Sea area. They apparently did not survive in this channel.

Poeciliopsis gracilis (Heckel)—Porthole livebearer

Mearns (1975) reported the collection of four specimens of this species on 27 July 1974, from an irrigation canal near Mecca, Riverside County. He suggested the common name porthole live bearer. The specimens were identified by C. L. Hubbs. Later in the year Mearns collected additional specimens at the same site. The presence of recently born young, the wide range of sizes, and the persistence of the fish for at least a 4-month period suggested that P. gracilis was a reproducing resident of this canal. Introduction persumably was by direct release by aquarists or escapements from a nearby tropical fish farm. Additional collections have been made as late as 1978.

ATHERINIDAE—silverside family

Menidia beryllina (Cope)—inland silverside

The inland silverside, under the name Menidia audens Hay—Mississippi silverside, was introduced into the Blue Lakes and Clear Lake in Lake

County in 1967 to test its effectiveness in controlling the Clear Lake gnat and chironomid midges (Cook and Moore 1970). These fish were obtained from Lake Texoma, Oklahoma. The former plant was authorized by the Fish and Game Commission whereas the latter was not. About 6,000 fish were released in upper Blue Lake and 3,000 in lower Blue Lake and Clear Lake. Within a year progeny from the original plant were abundant in the two latter lakes, and since then a virtual population explosion of silversides has taken place.

A combination of experimental introductions by the Department of Fish and Game, illegal introductions by bait fishermen, and dispersal via man-made waterways has resulted in wide distribution of this species. Moyle, Fisher, and Li (1974) reported the presence of silversides in Putah and Cache creeks in Yolo County and in eight reservoirs and ponds in Alameda and Santa Clara counties. Collections described by Meinz and Mecum (1977) demonstrated the occurrence of an abundant, reproducing population in the Sacramento-San Joaquin Delta. From here they have ready access to the California Aqueduct, the Delta-Mendota Canal, and associated water storage and conveyance systems and eventually southern California reservoirs.

SYNGNATHIDAE—pipefish family

Syngnathus _leptorhynchus_ Girard—bay pipefish

The bay pipefish has been recorded from the mouth of the San Lorenzo River, Santa Cruz County, and from the Navarro River, Mendocino County (Moyle 1976:283).

COTTIDAE--sculpin family

Cottus _perplexus_ Gilbert and Evermann—reticulate sculpin

A collection of reticulate sculpin was made from the Middle Fork of the Applegate River (Rogue River drainage) in California on 2 March 1971, by F. H. Everest and recorded by Bond (1973). *Cottus perplexus* is the most abundant representative of the genus in the Rogue. It is not known from coastal streams south of the Rogue.

Cottus pitensis Bailey and Bond—Pit sculpin

Bailey and Bond (1963) described this sculpin as a new species. This common species of the Pit River system in northeastern California had been collected frequently over the years but had been treated as *Cottus gulosus* except by Bond (1961).

PERCICHTHYIDAE—temperate bass family

Roccus chrysops (Rafinesque)—white bass

Von Geldern (1966) described the original introductions of white bass into California by the California Department of Fish and Game. About 160 fingerlings were planted in Nacimiento Reservoir, San Luis Obispo County, in November 1965 and 64 adults were released in the same water in February 1966. The former group were seined from Lake McConaughy in Nebraska and the latter from Tenkiller Reservoir in Oklahoma. Additional plants in Nacimiento included 600 yearlings and adults in July 1968 from Lahontan Reservoir in Nevada and 200 adults in February 1967 from Utah Lake in Utah. The Nacimiento population is now well established.

The California Department of Fish and Game and the Arizona Game and Fish Department cooperated in a series of plants of white bass in the lower Colorado River in 1968 and 1969. However, the species failed to become established in this location.

The popularity of white bass at Nacimiento Reservoir has led to illegal introductions into other waters of the State. One such water is Kaweah Reservoir, Tulare County, where it is firmly established.

CENTRARCHIDAE—sunfish family

Lepomis gulosus (Cuvier)—warmouth

The warmouth was designated Chaenobrythus gulosus in our 1959 list. However, for reasons described by Bailey et al. (1970:75), we believe that gulosus should be regarded as a species of Lepomis.

Lepomis macrochirus purpurescens Cope—southeastern bluegill

In June 1975, 88 subadult southeastern bluegill were stocked in Perris Lake, Riverside County, by the California Department of Fish and Game (Henry 1979). They were obtained through the cooperation of the Florida Game and Fresh Water Fish Commission from one of its hatcheries. They have reproduced and are firmly established. Specimens have been collected from Perris Lake and stocked in several small ponds for experimental purposes and to provide broodstock for future plants.

Micropterus coosae Hubbs and Bailey—redeye bass

Kimsey (1954) recorded the original importation of 40 specimens into California for use as broodstock by the California Department of Fish and Game. They were taken to Central Valleys Hatchery, Elk Grove, California. Kimsey (1957) reviewed the history of this introduction and its status and concluded, "No redeye bass were planted in the open waters of the State and none are now present in California."

A second attempt to establish the redeye bass in California was successful (Goodson 1966). Broodstock was imported from Tennessee and Georgia in the spring of 1968. These fish were spawned successfully at Central Valleys Hatchery and the progeny stocked in seven widely separated waters in the State: Lake Oroville, Butte County; Alder Creek, Sacramento County; South Fork Stanislaus River, Tuolumne County; Dry Creek, Nevada County; Santa Ana River, Riverside County; Sisquoc River, Santa Barbara County; and Santa Margarita River, San Diego County. Several thousand fingerlings and yearlings were stocked in these waters. It appears that only the Lake Oroville and South Fork Stanislaus River populations are firmly established (Lambert 1980). The remainder apparently did not survive.

Micropterus punctulatus henshalli Hubbs and Bailey—Alabama spotted bass

This species is thriving in Perris Lake, Riverside County. The original introduction consisted of 94 2-year-old individuals stocked by the California Department of Fish and Game in January 1974 (Brown, Aasen, and von Geldern 1977). An additional 29 fish were taken to the Department's Central Valleys Hatchery to provide a broodstock. These spotted bass were collected by the Alabama Department of Conservation and Natural Resources from Lewis Smith Lake.

Reproduction of bass held at Central Valleys Hatchery provided fish for a second introduction into Perris Lake in August 1974. In late 1974 between 2,000 and 3,000 fingerlings from this hatchery were stocked in Millerton Lake, Fresno County. This stocking was supplemented with 150 adults collected from Perris Lake in early 1975. Another 300 adults and subadults were collected from Perris Lake in March and April 1977 and released in San Vicente Reservoir, San Diego County. Both the Millerton and San Vicente populations are successfully established. Additional bass from Perris have since been stocked in New Hogan Reservoir, Calaveras County; Lake Isabella, Kern County; and Lake Oroville, Butte County.

Micropterus salmoides salmoides (Lacepède)—northern largemouth bass

Micropterus salmoides floridanus (Lesueur)—Florida largemouth bass

The nominate subspecies is the form widely distributed throughout the State. The Florida largemouth bass was imported into California in May 1959. A shipment of 20,400 fingerlings from Holt State Fish Hatchery near Pensacola, Florida, was planted in upper Otay Reservoir, San Diego County, on an experimental basis (Sasaki 1961; Bottroff and Lembeck 1978). A self-sustaining population was soon established and transplants were made to other San Diego County reservoirs. It is now established in other waters in the State.

PERCIDAE—perch family

Percina macrolepida Stevenson—bigscale logperch

In our 1959 checklist we listed and described the introduction of *Percina caprodes*, the logperch, into California. Since then, Stevenson (1971) described the bigscale logperch from Texas. Subsequent examination of specimens from California revealed them to be *P. macrolepida* rather than *P. caprodes* (Sturgess 1976).

EMBIOTOCIDAE—surfperch family

Hysterocarpus traskii traskii Gibbons—Sacramento tule perch

Hysterocarpus traskii lagunae Hopkirk—Clear Lake tule perch

Hysterocarpus traskii pomo Hopkirk—Russian River tule perch

Hopkirk revised the genus *Hysterocarpus*. He described the tule perch from the Russian River as a new subspecies and remarked, "The subspecies *pomo* is adapted for existence in small rivers. In body shape and in certain meristic characters, it represents an evolutionary parallel, not a relative, of the nominate subspecies." In his description of the new subspecies of tule perch from the Clear Lake Basin in central California, Hopkirk noted that it "...is adapted for pelagic or lacustrine existence, as evidenced by the alternate body, higher number of gill rakers, and silvery coloration." Remaining populations in the State are apparently referable to the nominate subspecies.

CICHLIDAE—cichlid family

Tilapia mossambica Peters—Mozambique tilapia

The first breeding population of this tilapia species in California was discovered in 1964 in a small pond and its tributary near the Salton Sea in Imperial County (St. Amant 1966). This population, which may no longer exist, probably originated from a nearby tropical fish farm. Subsequent authorized introductions in various ponds and waterways in the late 1960's and early 1970's for mosquito and aquatic weed control purposes, plus unauthorized introductions and natural movement of fish from one area to another, has culminated in the establishment of the Mozambique tilapia in southern California.

Hoover and St. Amant (1970) observed free-living populations of *T. mossambica* in irrigation canals and drains in Bard Valley, Imperial County in 1968. They remain abundant there as well as in similar habitat in the Palo Verde area, Imperial and Riverside counties. Isolated populations have been reported from drains in the Imperial Valley, Imperial County, and the Coachella Valley, Riverside County. Lake Elsinore in Riverside County and the Salton Sea support abundant, reproducing populations. The identity of tilapia from the Salton Sea remains uncertain, having been identified by various specialists as *T. mossambica*, *T. guineensis*, or *T. aurea*.

In recent years (*T. mossambica*) has established breeding populations in a series of watercourses entering the Pacific Ocean in Orange and Los Angeles counties (Knaggs 1977). They are concentrated in the estuarine portion of various flood control channels and channelized river beds such as the Los Angeles, Santa Ana, and San Gabriel rivers.

Tilapia zillii (Gervais)—redbelly tilapia

The redbelly tilapia was one of three tilapia species authorized by the Fish and Game Commission in 1971 for use in California. Its purported ability to control aquatic weeds was responsible for the interest in this species. During the early 1970's, it was stocked in several ponds in central California and in numerous ponds, canals, and drains in southern California. Except for the very southeastern corner of the State, it was believed that *T. zillii* could not survive winter temperatures and that small fish would have to be introduced periodically to achieve weed control. However, until killed by the exceptionally cold winter of 1972-73, they overwintered in the central California ponds. It was this unexpected tolerance to cold temperatures that prompted the Fish and Game Commission to place the redbelly tilapia on the prohibited species list for that portion of the State north of the Tehachapi Mountains.

Stocking in southern California, on the other hand, led to the permanent establishment of *T. zillii* and the likelihood of further spread of this highly adaptable species. They are abundant and breeding in all drains entering the Salton Sea and are also abundant in the Sea itself (Black 1980). They are likely to be encountered in certain canals and ditches in Bard and Imperial valleys, Imperial County, and in the

Coachella Valley, Riverside County. Breeding populations have been discovered in four backwaters of the Colorado River downstream from the Palo Verde Diversion Dam and in Lake Cahuilla, Riverside County. Two specimens have been reported from the marine environment near Huntington Beach and in Newport Bay, Orange County (Knaggs 1977).

GOBIIDAE—goby family

Acanthogobius flavimanus (Temminck and Schlegel)—yellowfin goby

This species was first collected by personnel of the California Department of Fish and Game in the San Joaquin River off Prisoners Point on 18 January 1963 (Brittan, Albrecht, and Hopkirk 1963). It soon spread rapidly (Brittan et al. 1970) and is now widely established in the Sacramento-San Joaquin Delta and San Francisco Bay area. The origin of these fish is not known, but it may have been carried in a ship's seawater system.

Tridentiger trigonocephalus (Gill)—chameleon goby

Miller and Lea (1972) list this species as occurring in the shallows of both the Los Angeles Harbor and San Francisco Bay. They state that it was inadvertently introduced from the Orient. Moyle (1976) remarks that it, "...has not yet been collected in fresh water in California but can be expected there, since it occurs in brackish Lake Merritt in Oakland and in the lower reaches of streams in its native Asia." Hubbs and Miller (1965:44), however, refer to data indicating that Lake Merritt is a freshwater lake, although it connects directly with San Francisco Bay.

Forms and Names Removed from the Main List Since 1959

PETROMYZONTIDAE—lamprey family

Lampetra planeri (Bloch)—brook lamprey

Vladykov and Follett (1965) described Lampetra richardsoni, a new nonparasitic species of lamprey from "streams of British Columbia, Washington, Oregon, and possibly Alaska." Follett subsequently informed J. D. Hopkirk (pers. commun.), that the range of L. richardsoni, the western brook lamprey, was more recently known to include California. Various authors had previously listed this species as L. planeri, the name used in our 1959 checklist.

OSMERIDAE—smelt family

Hypomesus olidus (Pallas)—pond smelt

The fish which we listed in our 1959 checklist under this name has since been described as a new species, H. transpacificus, by McAllister (1963).

SALMONIDAE—salmon and trout family

Salmo clarkii evermanni Jordan and Grinnell—San Gorgonio cutthroat trout

After finding a record that cutthroat trout from Lake Tahoe had been planted in the stream from which Salmo evermanni was later obtained, Benson and Behnke (1961) closely compared the type and two "cotypes" of evermanni with specimens of Salmo clarkii henshawi from Lake Tahoe. They found no significant differences and concluded that evermanni was a synonym.

Salmo gairdnerii regalis Snyder—royal silver rainbow trout

La Rivers (1962) questioned the taxonomic validity of both S. g. regalis of Lake Tahoe and S. g. smaragdus of Pyramid Lake. He argues convincingly against the acceptance of these rainbow subspecies as Great Basin endemics, believing that the specimens examined by Snyder (1914, 1918) were probably either introduced rainbow or rainbow-cutthroat hybrids. Widespread stocking of rainbow trout beginning in the 1860's in the Lahontan system, was likely the original source of these specimens.

One of us (Cordone) collected 226 rainbow trout from the limnetic zone of Lake Tahoe in the early 1960's. Seventy-three of these were marked fish, survivors from plants of hatchery-reared rainbow. Many of these specimens, both marked and unmarked, possessed the phenotypic appearance of the royal silver trout noted by Snyder (1918), "It is distinguished by the absence of spots, by the blue or green dorsal surface, the silvery sides and white belly, and the loose scales which, when the fish is caught, adhere to the fingers like bits of foil." Behnke (1972) examined some of these specimens and concluded, "The silvery, smoltlike appearance, supposedly diagnostic for _S. regalis_ can be duplicated by hatchery rainbow trout after a period of life in Lake Tahoe."

CYPRINIDAE—carp or minnow family

Pimephales promelas confertus (Girard)—southwestern flathead minnow

We follow Taylor (1954:42) and Vandermeer (1966:465) in not recognizing subspecies in _Pimephales promelas_, primarily because most of the variation over its range appears to be clinal. Even if subspecies were recognized, the populations of the fathead minnow in California are from such diverse out-of-state localities that it would be difficult to single out subspecies.

Plagopterus argentissimus Cope—woundfin

This species, native to the Colorado River system, is now only occasionally found in Arizona portions of the system and may never have occurred in the California portion.

Rhinichthys osculus carringtonii (Cope)—Pacific speckled dace

W. I. Follett (pers. commun.) states: "We are not recognizing _Rhinichthys osculus carringtonii_ (originally described from Warm Springs, Box Elder County, Utah) as occurring in California. Dr. Hubbs now regards as a misidentification *Agosia nubila carringtonii* Culver and Hubbs, 1917, Lorquinia, 1(2):83, from Santa Ana River, California." On this basis we are dropping this form from our list.

Siphateles bicolor formosus (Girard)—Sacramento tui chub

If this were a valid subspecies, its current name would be *Gila bicolor formosa*. Moyle (1976:164) comments on it as follows: "The name *G. b. formosa* was originally applied to tui chubs that were supposed to have lived in the Sacramento-San Joaquin Valley. Since only a few poorly preserved specimens of the form are known, the subspecies may be based on a mislabeled collection (C. L. Hubbs, pers. commun.)." For these reasons, we are dropping this form from the main list.

CATOSTOMIDAE—sucker family

Catostomus latipinnis Baird and Girard—flannelmouth sucker

This species, native to the Colorado River system, is now found only upstream from Lake Mead (Minckley 1973:157). Like *Plagopterus argentissimus*, it may never have occurred in the California portion of the Colorado River except for an occasional specimen washed down from upstream waters.

Ictiobus cyprinella (Valenciennes)—bigmouth buffalo

This exotic species was included in the first two lists on the basis of its occurrence in several reservoirs of the Los Angeles Aqueduct system in Los Angeles and Inyo counties. However, none have been collected from these waters since the late 1960's and they probably no longer exist in the State (F. G. Hoover, pers. commun.). Since this species, along with the black buffalo, *Ictiobus niger*, and the smallmouth buffalo, Ictiobus bubalus, are present in Arizona waters, they may be expected on occasion to find their way into the lower Colorado River and connected waters. C. L. Hubbs identified a specimen of I. bubalus collected by J. A. St. Amant in 1969 from a waterway in southern California.

Pantosteus lahontan Rutter—Lahontan mountain-sucker

Smith (1966) united Pantosteus lahontan and P. platyrhynchus as Catostomus platyrhynchus, which replaces P. lahontan in our present list.

ICTALURIDAE—North American freshwater catfish family

Ictalurus melas melas (Rafinesque)—northern black bullhead

Ictalutus natalis natalis (Lesueur)—northern yellow bullhead

Ictalurus nebulosus nebulosus (Lesueur)—northern brown bullhead

We follow Hubbs et al. (1979) and Bailey (1956:328-329; pers. commun.) in dropping recognition of these trinomials. They were described without documentation and may represent only clinal variations.

CENTRARCHIDAE—sunfish family

Micropterus dolomieu dolomieu Lacepède—northern smallmouth bass

We follow Hubbs et al. (1979) and Bailey (1956:328-329, pers. commun.) in dropping recognition of this trinomial. It was described without adequate documentation and may represent only clinal variation.

ELEOTRIDAE—sleeper family

Eleotris picta Kner and Steindachner—spotted sleeper O

This species was added to the 1959 list on the basis of a single specimen caught by a fisherman at the canal spillway between Winterhaven and the Colorado River in Imperial County (Hubbs 1953). However, none have been taken from California fresh waters since that time (Minckley 1973:259; Moyle 1976:70).

REVISED MAIN LIST

Native Species and Established Exotic Species

This revised list consists of 124 full species, which may be subdivided as follows: 66 native freshwater and anadromous species, 13 native marine or euryhaline species which occasionally penetrate into fresh water, and 45 introduced species. The 124 species comprise 25 families and 64 genera.

Species which have been introduced into California waters are denoted by an asterisk (*), and marine or euryhaline fishes which occur occasionally in fresh water by an "O".

PETROMYZONTIDAE—lamprey family

1. _Lampetra ayressi_ (Günther)—river lamprey
2. _Lampetra folletti_ (Vladykov and Kott)—Modoc brook lamprey
3. _Lampetra hubbsi_ (Vladykov and Kott)—Kern brook lamprey
4. _Lampetra lethophaga_ Hubbs—Pit-Klamath brook lamprey
5. _Lampetra pacifica_ Vladykov—Pacific brook lamprey
6. _Lampetra richardsoni_ Vladykov and Follett—western brook lamprey
7. _Lampetra tridentata_ (Gairdner)—Pacific lamprey

ACIPENSERIDAE—sturgeon family

8. _Acipenser medirostris_ Ayres—green sturgeon
    8a. _Acipenser medirostris medirostris_ Ayres—American green sturgeon
9. _Acipenser transmontanus_ Richardson—white sturgeon

ELOPIDAE—tenpounder family

10. _Elops affinis_ Regan—machete O

CLUPEIDAE—herring family

11. *Alosa sapidissima* (Wilson)—American shad *

12. *Clupea harengus* Linnaeus—herring O

    12a. *Clupea harengus pallasii* Valenciennes—Pacific herring O

13. *Dorosoma petenense* (Günther)—threadfin shad *

OSMERIDAE—smelt family

14. *Hypomesus nipponensis* McAllister—freshwater smelt *

15. *Hypomesus pretiosus* (Girard)—surf smelt O

16. *Hypomesus transpacificus* McAllister—delta smelt

17. *Spirinchus thaleichthys* (Ayres)—longfin smelt O

18. *Thaleichthys pacificus* (Richardson)—eulachon

COREGONIDAE—whitefish family

19. *Prosopium williamsoni* (Girard)—mountain whitefish

SALMONIDAE—salmon and trout family

20. *Oncorhynchus gorbuscha* (Walbaum)—pink salmon

21. *Oncorhynchus keta* (Walbaum)—chum salmon

22. *Oncorhynchus kisutch* (Walbaum)—coho salmon (silver salmon)

23. *Oncorhynchus nerka* (Walbaum)—sockeye salmon (anadromous form); kokanee salmon (freshwater form *)

24. *Oncorhynchus tshawytscha* (Walbaum)—chinook salmon (king salmon)

25. *Salmo aguabonita* Jordan—golden trout

    25a. *Salmo aguabonita aguabonita* Jordan—South Fork Kern golden trout

    25b. *Salmo aguabonita whitei* Evermann—Little Kern golden trout

26. *Salmo clarkii* Richardson—cutthroat trout

    26a. *Salmo clarkii clarkii* Richardson—coast cutthroat trout

    26b. *Salmo clarkii henshawi* Gill and Jordan—Lahontan cutthroat trout

26c. Salmo clarkii pleuriticus Cope—Colorado River cutthroat trout

26d. Salmo clarkii seleniris Snyder—Paiute cutthroat trout

27. Salmo gairdnerii Richardson—rainbow trout

27a. Salmo gairdnerii gairdnerii Richardson—steelhead rainbow trout

27b. Salmo gairdnerii aquilarum Snyder—Eagle Lake rainbow trout

27c. Salmo gairdnerii gilberti Jordan—Kern River rainbow trout

27d. Salmo gairdnerii kamloops (Jordan)—Kamloops rainbow trout *

27e. Salmo gairdnerii stonei Jordan—Shasta rainbow trout

28. Salmo trutta Linnaeus—brown trout *

29. Salvelinus confluentus (Suckley)—bull trout

30. Salvelinus fontinalis (Mitchill)—brook trout *

31. Salvelinus malma (Walbaum)—Dolly Varden

32. Salvelinus namaycush (Walbaum)—lake trout *

32a. Salvelinus namaycush namaycush (Walbaum)—common lake trout *

CYPRINIDAE—carp or minnow family

33. Carassius auratus (Linnaeus)—goldfish *

34. Cyprinus carpio Linnaeus—carp *

35. Gila bicolor (Girard)—tui chub

35a. Gila bicolor bicolor (Girard)—Klamath tui chub

35b. Gila bicolor mohavensus (Snyder)—Mohave tui chub

35c. Gila bicolor obesa (Girard)—Lahontan coarseraker tui chub

35d. Gila bicolor pectinifer (Snyder)—Lahontan fineraker tui chub

35e. Gila bicolor snyderi Miller—Owens tui chub

35f. Gila bicolor thalassina (Cope)—Goose Lake tui chub

35g. Gila bicolor vaccaceps Bills and Bond—Cowhead Lake tui chub

36. Gila coerulea (Girard)—blue chub

37. Gila crassicauda (Baird and Girard)—thicktail chub

38. Gila elegans Baird and Girard—bonytail chub

39. Gila orcuttii (Eigenmann and Eigenmann)—arroyo chub

40. Hesperoleucus symmetricus (Baird and Girard)—western roach

    40a. Hesperoleucus symmetricus symmetricus (Baird and Girard)—Sacramento western roach

    40b. Hesperoleucus symmetricus mitrulus Snyder—upper Pit western roach

    40c. Hesperoleucus symmetricus navarroensis Snyder—Navarro western roach

    40d. Hesperoleucus symmetricus parvipinnis Snyder—Gualala western roach

    40e. Hesperoleucus symmetricus subditus Snyder—Monterey western roach

    40f. Hesperoleucus symmetricus venustus Snyder—Venus western roach

41. Lavinia exilicauda Baird and Girard—hitch

    41a. Lavinia exilicauda exilicauda Baird and Girard—Sacramento hitch

    41b. Lavinia exilicauda chi Hopkirk—Clear Lake hitch

    41c. Lavinia exilicauda harengus Girard—Monterey hitch

42. Mylopharodon conocephalus (Baird and Girard)—hardhead

43. Notemigonus crysoleucas (Mitchill)—golden shiner *

44. Notropis lutrensis (Baird and Girard)—red shiner *

45. Orthodon microlepidotus (Ayres)—Sacramento blackfish

46. Pimephales promelas Rafinesque—fathead minnow *

47. Pogonichthys ciscoides Hopkirk—Clear Lake splittail

48. Pogonichthys macrolepidotus (Ayres)—Sacramento splittail

49. Ptychocheilus grandis (Ayres)—Sacramento squawfish

50. Ptychocheilus lucius Girard—Colorado squawfish

51. Rhinichthys osculus (Girard)—speckled dace

51a. Rhinichthys osculus klamathensis (Evermann and Meek)—Klamath speckled dace

51b. Rhinichthys osculus nevadensis Gilbert—Amargosa speckled dace

51c. Rhinichthys osculus robustus (Rutter)—Lahontan speckled dace

52. Richardsonius egregius (Girard)—Lahontan redside

53. Tinca tinca (Linnaeus)—tench *

CATOSTOMIDAE—sucker family

54. Catostomus fumeiventris Miller—Owens sucker

55. Catostomus luxatus (Cope)—Lost River sucker

56. Catostomus microps Rutter—Modoc sucker

57. Catostomus occidentalis Ayres—western sucker

57a. Catostomus occidentalis occidentalis Ayres—Sacramento western sucker

57b. Catostomus occidentalis humboldtianus Snyder—Humboldt western sucker

57c. Catostomus occidentalis lacusanserinus Fowler—Goose Lake western sucker

57d. Catostomus occidentalis mniotiltus Snyder—Monterey western sucker

58. Catostomus platyrhynchus (Cope)—mountain sucker

59. Catostomus rimiculus Gilbert and Snyder—Klamath smallscale sucker

60. Catostomus santaanae (Snyder)—Santa Ana sucker

61. Catostomus snyderi Gilbert—Klamath largescale sucker

62. Catostomus tahoensis Gill and Jordan—Tahoe sucker

63. Chasmistes brevirostris Cope—shortnose sucker

64. Xyrauchen texanus (Abbott)—humbpack sucker

COBITIDAE—loach family

65. Misgurnus anguillicaudatus (Cantor)—Oriental weatherfish *

ICTALURIDAE--North American freshwater catfish family

66. Ictalurus catus (Linnaeus)—white catfish *

67. Ictalurus furcatus (Lesueur)—blue catfish *

68. Ictalurus melas (Rafinesque)—black bullhead *

69. Ictalurus natalis (Lesueur)—yellow bullhead *

70. Ictalurus nebulosus (Lesueur)—brown bullhead *

71. Ictalurus punctatus (Rafinesque)—channel catfish *

72. Pylodictis olivaris (Rafinesque)—flathead catfish *

CYPRINODONTIDAE—killifish family

73. Cyprinodon macularius Baird and Girard—desert pupfish

73a. Cyprinodon macularius macularius Baird and Girard—Colorado Basin desert pupfish

73b. Cyprinodon macularius californiensis Girard—San Diego desert pupfish

74. Cyprinodon milleri LaBounty and Deacon—Cottonball Marsh pupfish

75. Cyprinodon nevadensis Eigenmann and Eigenmann—Nevada pupfish

75a. Cyprinodon nevadensis nevadensis Eigenmann and Eigenmann—Saratoga pupfish

75b. Cyprinodon nevadensis amargosae Miller—Amargosa Nevada pupfish

75c. Cyprinodon nevadensis calidae Miller—Tecopa Nevada pupfish

75d. Cyprinodon nevadensis shoshone Miller—Shoshone Nevada pupfish

76. Cyprinodon radiosus Miller—Owens pupfish

77. Cyprinodon salinus Miller—Salt Creek pupfish

78. Fundulus parvipinnis Girard—California killifish

78a. Fundulus parvipinnis parvipinnis—southern California killifish

79. Lucania parva (Baird and Girard)—rainwater killifish *

POECILIIDAE—livebearer family

80. Gambusia affinis (Baird and Girard)—mosquitofish *

    80a. Gambusia affinis affinis (Baird and Girard)—western mosquitofish *

81. Poecilia latipinna (Lesueur)—sailfin molly *

82. Poecilia mexicana Steindachner—shortfin molly *

    82a. Poecilia mexicana mexicana Steindachner—Orizaba shortfin molly *

83. Poeciliopsis gracilis (Heckel)—porthole livebearer *

ATHERINIDAE—silverside family

84. Atherinops affinis (Ayres)—topsmelt O

85. Menidia beryllina (Cope)—inland silverside *

GASTEROSTEIDAE—stickleback family

86. Gasterosteus aculeatus Linnaeus—threespine stickleback

    86a. Gasterosteus aculeatus aculeatus Linnaeus—armored threespine stickleback

    86b. Gasterosteus aculeatus microcephalus Girard—semiarmored threespine stickleback

    86c. Gasterosteus aculeatus williamsoni Girard—unarmored threespine stickleback

SYNGNATHIDAE—pipefish family

87. Syngnathus leptorhynchus Girard—bay pipefish O

COTTIDAE—sculpin family

88. Clinocottus acuticeps (Gilbert)—sharpnose sculpin O

89. Cottus aleuticus Gilbert—coastrange sculpin

90. Cottus asper Richardson—prickly sculpin

91. Cottus asperrimus Rutter—rough sculpin

92. _Cottus beldingii_ Eigenmann and Eigenmann—Paiute sculpin

93. _Cottus gulosus_ (Girard)—riffle sculpin

94. _Cottus klamathensis_ Gilbert—marbled sculpin

95. _Cottus perplexus_ Gilbert and Evermann—reticulate sculpin

96. _Cottus pitensis_ Bailey and Bond—Pit sculpin

97. _Leptocottus armatus_ Girard—Pacific staghorn sculpin O

    97a. _Leptocottus armatus armatus_ Girard—northern Pacific staghorn sculpin O

    97b. _Leptocottus armatus australis_ Hubbs—southern Pacific staghorn sculpin O

PERCICHTHYIDAE—temperate bass family

98. _Roccus chrysops_ (Rafinesque)—white bass *

99. _Roccus saxatilis_ (Walbaum)—striped bass *

CENTRARCHIDAE—sunfish family

100. _Archoplites interruptus_ (Girard)—Sacramento perch

101. _Lepomis cyanellus_ Rafinesque—green sunfish *

102. _Lepomis gibbosus_ (Linnaeus)—pumpkinseed *

103. _Lepomis gulosus_ (Cuvier)—warmouth *

104. _Lepomis macrochirus_ Rafinesque—bluegill *

    104a. _Lepomis macrochirus macrochirus_ Rafinesque—northern bluegill *

    104b. _Lepomis macrochirus purpurescens_ Cope—southeastern bluegill *

105. _Lepomis microlophus_ (Gunther)—redear sunfish *

106. _Micropterus coosae_ Hubbs and Bailey—redeye bass *

107. _Micropterus dolomieu_ Lacepède—smallmouth bass *

108. _Micropterus punctulatus_ (Rafinesque)—spotted bass *

    108a. _Micropterus punctulatus punctulatus_ (Rafinesque)—northern spotted bass *

108b. Micropterus punctulatus henshalli Hubbs and Bailey—Alabama spotted bass *

109. Micropterus salmoides (Lacepède)—largemouth bass *

109a. Micropterus salmoides salmoides (Lacepède)—northern largemouth bass *

109b. Micropterus salmoides floridanus (Lesueur)—Florida largemouth bass *

110. Pomoxis annularis Rafinesque—white crappie *

111. Pomoxis nigromaculatus (Lesueur)—black crappie *

PERCIDAE—perch family

112. Perca flavescens (Mitchill)—yellow perch *

113. Percina macrolepida Stevenson—bigscale logperch *

EMBIOTOCIDAE—surfperch family

114. Cymatogaster aggregata Gibbons—shiner perch O

115. Hysterocarpus traskii Gibbons—tule perch

115a. Hysterocarpus traskii traskii Gibbons—Sacramento tule perch

115b. Hysterocarpus traskii lagunae Hopkirk—Clear Lake tule perch

115c. Hysterocarpus traskii pomo Hopkirk—Russian River tule perch

CICHLIDAE—cichlid family

116. Tilapia mossambica (Peters)—Mozambique tilapia *

117. Tilapia zillii (Gervais)—redbelly tilapia *

MUGILIDAE—gray mullet family

118. Mugil cephalus Linnaeus—striped mullet O

GOBIIDAE—goby family

119. Acanthogobius flavimanus (Temminck and Schlegel)—yellowfin goby *

120. Clevelandia ios (Jordan and Gilbert)—arrow goby O

121. Eucyclogobius newberryi (Girard)—tidewater goby

122. Gillichthys mirabilis Cooper—longjaw mudsucker O

123. Tridentiger trigonocephalus (Gill)—chameleon goby O*

PLEURONECTIDAE—righteye flounder family

124. Platichthys stellatus (Pallas)—starry flounder O

124a. Platichthys stellatus rugosus Girard—southern starry flounder O

REVISED SUPPLEMENTARY LISTS

Native Species—Extinct or Extirpated from California

SALMONIDAE—salmon and trout family

The following native fishes apparently no longer exist in California and are either extinct, or if they still exist outside of the State, are considered extirpated. Nine extinct or extirpated species fit this description. We included only those species which at one time were well established. Not included are Plagopterus argentissimus and Catostomus latipinnis, which rarely, if ever, entered California waters. Also left out is the Clear Lake minnow, Endemichthys grandipinnis, which was described by Hopkirk (1973:57). He observed that it was apparently extinct, but has since found cause to reconsider the validity of this species (Hubbs et al. 1979).

Salvelinus confluentus (Suckley)—bull trout

Salvelinus malma (Walbaum)—Dolly Varden

These species (there is some question that at one time both existed in the McCloud River) have likely been extirpated from California due to man-made environmental changes and the introduction of exotic trout into the McCloud River drainage. The last known specimens, probably bull trout, were taken in 1975 (Moyle 1976:146). Intensive sampling of the McCloud River and its tributaries in recent years has failed to locate either species (S. J. Nicola, Senior Fishery Biologist, Calif. Dep. Fish and Game, pers. commun.).

CYPRINIDAE—carp or minnow family

Gila crassicauda (Baird and Girard)—thicktail chub

This chub was once common in the Central Valley, Clear Lake in Lake County, and at least one tributary to south San Francisco Bay. The combination of man-caused habitat changes and the introduction of exotic fishes has led to its apparent extinction (Miller 1963). The California Department of Fish and Game (1978) reports that the last known specimen was taken in 1957 from Steamboat Slough in the Sacramento River Delta. Moyle (1976:172), however, states that the last specimen was collected from Cache Slough, near Rio Vista, in 1958.

Gila elegans Baird and Girard—bonytail chub

This species, listed in our 1959 list as *Gila robusta elegans*, Colorado River bonytail chub, has not been found in the California portion of the Colorado River in recent years and may be considered extirpated from the State (Colorado River Wildlife Council 1977; Calif. Dep. Fish and Game 1978).

Pogonichthys ciscoides Hopkirk—Clear Lake splittail

It was not until Hopkirk (1973) published the results of his studies that the Clear Lake splittail was recognized as a distinct species. By this time it was probably already extinct. Cook, Moore, and Conners (1966) described the early history of the species. It was very abundant until the early 1940's, when it declined drastically. Occasional resurgences did nothing to halt the overall decline and apparently none have been collected since the late 1960's. Once again, habitat destruction and exotic fishes are responsible for extinction.

Ptychocheilus lucius Girard—Colorado squawfish

Although still present in a few localities in the upper Colorado River drainage, the Colorado squawfish apparently has been extirpated from California waters. It was once abundant in the lower Colorado River but by the early 1960's was probably already extirpated (Moyle 1976:195). It has not been collected since 1952 (Calif. Dep. Fish and Game 1978). Environmental degradation and exotic fishes are again believed responsible for the loss.

CYPRINODONTIDAE—killifish family

Cyprinodon macularius californiensis Girard—San Diego desert pupfish

Little is known about this subspecies other than the description given by Girard (1860). It was reportedly collected in the neighborhood of the City of San Diego. Lack of subsequent collections and intensive urbanization of this area leave little doubt that it is extinct.

Cyprinodon nevadensis calidae Miller—Tecopa Nevada pupfish

This subspecies, originally from north and south Tecopa Hot Springs, Inyo County, has become extinct in recent years (Moyle 1976:256), as a result of activities by man which led to destruction of its habitat.

Cyprinodon nevadensis shoshone Miller—Shoshone Nevada pupfish

This subspecies, from Shoshone Springs, Inyo County, like C. n. calidae, has become extinct in recent years (Moyle 1976:256), as a result of activities by man leading to destruction of its habitat.

Exotic Species—Unsuccessfully Introduced or of Uncertain Status

It is extremely difficult to establish rigid criteria for the inclusion or exclusion of fishes in this section. Some situations are obvious. For example, we have included a species in this section, if it was introduced as part of a planned program or if there was a large escapement of the species from a tropical fish farm, or elsewhere, and subsequent investigations have shown with reasonable certainty that it is no longer present. On the other hand, if only a single specimen or a very few specimens, even if positively identified, were recorded we have omitted such species from this section. Obviously, these are judgmental assessments.

The occurrence of a single or a few specimens of tropical fishes probably represent releases by home aquarists. Brittan and Grossman (1979) describe a specimen of pacu, Colossoma sp., caught by an angler in 1977 from the Sacramento River in Yolo County. Another pacu was reportedly taken from the California Aqueduct in 1979 (Calif. Dep. Fish and Game, Region 5 monthly report for November 1979). Minckley (1973: 185) refers to a specimen of walking catfish, Clarias batrachus, taken by an angler from the All American Canal west of Yuma, Arizona. A South American aruana, Osteoglossum bicirrhosum, was caught by an angler in Lake Berryessa (Calif. Dep. Fish and Game, Region 3 news release for June 18, 1972). Two mature tiger barbs, Barbus tetrazona, were collected in 1963 from the small stream flowing from Warm Springs Sanctuary in Owens Valley, Inyo County (Naiman and Pister 1974). None has been taken since then, despite repeated collecting efforts.

Escapement from tropical fish farms apparently has been the source of a number of established exotics, such as Misgurnus anguillicaudatus, Poecilia latipinna, P. mexicana, and Poeciliopsis gracilis. Other tropical species have escaped but in small numbers, and fortunately have not established permanent populations. For example, among the exotics collected by St. Amant and Hoover (1969) from the Westminster flood control channel in Orange County in 1968 were the guppy, Lebistes retuculatus; green swordtail, Xiphophorus hellerii; southern platyfish, X. maculatus; variable platyfish, X. variatus; shortfin molly, Poecilia mexicana; zebra danio, Brachydanio rerio; and angelfish, Pterophyllum sp. None of these has since been taken in this channel, despite repeated collecting attempts. Mearns (1975) took a specimen of Xiphophorus helleri in 1974 from a drain to the Salton Sea, but none was recorded in subsequent sampling.

The 1959 supplementary list included a number of species of bait minnows that were being utilized along the Colorado River (Miller 1952). None of these has become established and apparently are no longer being used, so we have deleted them.

The exotic fishes listed below fall into several groups:

1. Fishes known to have been introduced but which have not survived; e.g., No. 2.
2. Fishes reported, possibly erroneously, to have been introduced, but which have not survived; e.g., No. 9.
3. Fishes which have been reported from this State but whose identification is questioned by the authors; e.g., No. 21.
4. Fishes which have not been recorded from the State for many years; e.g., No. 23.

As will be seen by our annotations, we know of no demonstrable evidence that any of them are successfully established in the fresh waters of California today.

The general sources for the history and lack of success of most of these introductions are fairly well known. Therefore, there is little point in listing all the references concerning the status of these fishes. We have alluded to specific literature only when our opinion differs from that of the authors cited, or when such inclusion serves to clarify the exact status of the species.

ANGUILLIDAE—freshwater eel family

1. Anguilla rostrata (Lesueur)—American eel

Introduced in 1874, 1879, and 1882. There are no authentic records of survival. However, an occasional specimen is collected from various waters in the State. Skinner (1971) reported the capture of two eels from the Sacramento-San Joaquin Delta. The first was taken in 1964 and was identified by C. L. Hubbs as an American eel. The second was caught in 1969 and was identified as a European eel (Anguilla anguilla Linnaeus) by W. I. Follett. Skinner maintained that the most logical explanation for the occurrence of both eels is that they were transported from abroad in the ballast of commercial ships. In 1978 an unidentified species of Anguilla was captured in the Los Angeles River (J. A. St. Amant, Associate Fishery Biologist, Calif. Dep. Fish and Game, pers. commun.).

PLECOGLOSSIDAE—ayu family

2. Plecoglossus altivelis Temminck and Schlegel—ayu

Large numbers of eggs and fry of this native Japanese species were stocked in California on the recommendation of Dr. John W. DeWitt, Professor of Fisheries at Humboldt State University, Arcata. Following approval from the Fish and Game Commission, plants of this species were made annually from 1961 through 1965. About 3,845,000 eggs and fry were stocked during this period: 200,000 eggs and fry in Morris Lake, Mendocino County; 395,000 eggs in Ruth Reservoir, Trinity County; and 3,250,000 eggs and fry in the Eel River below Fortuna, Humboldt County (J. W. DeWitt, pers. commun.). The venture was unsuccessful, since no survivors were ever reported.

COREGONIDAE—whitefish family

3. _Coregonus clupeaformis_ (Mitchill)—lake whitefish

3a. _Coregonus clupeaformis clupeaformis_ (Mitchill)—Great Lakes whitefish

All plants were made during the last century. Even the few old reports of recapture (circa 1850) are considered highly dubious.

4. _Prosopium gemmiferum_ (Snyder)—Bonneville cisco

In January of 1964, 1965, and 1966, 21,506 spawning Bonneville cisco and about 250,000 cisco eggs were collected from Bear Lake, Utah-Idaho, and transported to Lake Tahoe (Frantz and Cordone 1965, 1967). About 205,000 green eggs, 3,000 eyed eggs and alevins, and 15,888 ripe adults were released alive in Lake Tahoe over the 3-year span. None are known to have survived.

SALMONIDAE—salmon and trout family

5. _Salmo clarkii_ Richardson—cutthroat trout

5a. _Salmo clarkii lewisi_ (Girard)—Yellowstone cutthroat trout

Several shipments of cutthroat trout eggs have been brought in from other states, and plants made in California waters. It is probable that most of them were _S. c. lewisi_.

6. _Salmo salar_ Linnaeus—Atlantic salmon (anadromous form); landlocked Atlantic salmon (freshwater form)

Both forms have been planted several times. The old records of their survival may be dubious; there are no authentic recent records.

7. _Thymallus arcticus_ (Pallas)—Arctic grayling

Several early attempts were made to introduce this form, and it apparently met with a brief success in Yosemite National Park following plants made during the 1929-1933 period. However, the last authentic report of its survival there (in Grayling Lake) appears to have been in 1934.

More recently, the California Department of Fish and Game imported large numbers of grayling eggs from Arizona and Wyoming. Resultant fry and fingerlings were stocked in 57 widely scattered high mountain lakes and one stream from the southern Sierra Nevada into northern California. Approximately 156,000 fish were released during the period 1969 to 1975. Good survival and growth were documented at many of these waters but actual reproduction has not been confirmed.

ESOCIDAE—pike family

8. _Esox americanus_ Gmelin—redfin pickerel

8a. _Esox americanus vermiculatus_ Lesueur—grass pickerel

9. _Esox lucius_ Linnaeus—northern pike

E. lucius was supposedly introduced in 1891, but one of the fish resulting from this shipment was identified in 1896 as _E. vermiculatus_ (now _E. a. vermiculatus_). Possibly both species were included. There are no records of capture of either species after 1896.

10. _Esox_ _masquinongy_ Mitchill—muskellunge

10a. _Esox_ _masquinongy_ _ohioensis_ Kirkland—Ohio muskellunge

Introduced into Lake Merced, San Francisco County, in 1893. None survived.

CHANIDAE—milkfish family

11. _Chanos_ _chanos_ (Forskal)—milkfish

Milkfish from the Hawaiian Islands were planted in a stream in Solano County in 1877. There are no records of their survival there. The species is an ocean fish which occasionally enters fresh water.

CYPRINIDAE—carp or minnow family

12. _Ctenopharyngodon_ _idella_ Valenciennes—grass carp

Illegal introductions of grass carp into California have been made in the past and may still be continuing. Despite the fact that this species is officially prohibited in the State, and thus may not be imported, transported, or possessed, farm pond owners have been importing grass carp from commercial fish farmers in Arkansas and Pennsylvania. The Department has thus far uncovered four instances of grass carp introductions; 12 fingerlings were released in a small pond in Ventura County in 1975, 48 fingerlings were planted in a small pond in El Dorado County in 1975, 2,800 fingerlings and 200 0.34 kg (3/4 lb) fish were released in seven ponds on a ranch in Napa County in 1975, and 20 grass carp fingerlings were stocked in a small pond in Mendocino County in 1978. The latter plant apparently did not survive the trip from Pennsylvania, but the remaining lots from Arkansas survived and were healthy and growing rapidly when they were removed by the Department.

In May 1980 about 850 hybrids of female grass carp and male bighead carp, Aristichthys nobilis, were released in several man-made waterways in the Coachella Valley. Further releases are anticipated as part of a study to assess the aquatic weed control potential of the hybrid.

ICTALURIDAE—North American freshwater catfish family

13. Ictalurus platycephalus (Girard)—flat bullhead

On the basis of a survey made in 1925, Coleman (1930) recorded "The Great Blue, or Forked-Tail Cat--Ictalurus furcatus, Cuv. and Vincen.," and "The Brown-Spotted Cat--Ameirus [sic.] platycephalus, Girard," from Clear Lake, Lake County. Neither has been recorded from the lake since that time, despite extensive collecting. We believe that Coleman confused Ictalurus catus (which is found in Clear Lake and which is often called "forked-tail catfish" or "blue cat") with his "furcatus". We suspect that his record of I. platycephalus is based upon his erroneous interpretation of fishermen's reports.

ORYZIATIDAE—tooth-carp family

14. Oryzias latipes (Temminck and Schlegal)—medaka

The statement by Snyder (1935), "It has been found in San Francisquito Creek", and Coates(1942:185), "...this fish has been turned loose in...parts of California, where it is reported to be thriving", are the sole bases for its admission to this list.
In a conversation with Snyder on 21 March 1943, he told us (Dill) that some of his students had collected this form in San

Francisquito Creek, Santa Clara County. He did not recall the date or other circumstances.

CYPRINODONTIDAE—killifish family

15. _Cynolebias bellottii_ Steindachner—Argentine pearlfish

This was the most widely used of the so-called "annual fishes" stocked in several locations in the State, principally in Butte, Kern, and Riverside counties, for mosquito control purposes. Bay (1966) described the first field tests with this species at the University of California, Riverside. Survivors of the tests contaminated the Riverside ponds for 5 years despite repeated floodings and dryings but finally died out (E. F. Legner, Entomologist, Univ. Calif., Riverside, pers. commun.). Additional field tests with the Argentine pearlfish were described by E. C. Bay (Superintendent, Western Wash. Res. and Extension Center, Washington St. Univ., pers. commun.). Field tests in experimental ponds were conducted in 1966 and 1967 in Kern and Butte counties. The results were negative and the species failed to become established.

Experimental rice plots and ponds on the grounds of the Butte County Mosquito Abatement District were the sites of tests conducted in 1973 and 1974 utilizing the black pearlfish, _Cynolebias nigripinnis_, and White's pearlfish, _Cynolebias whitei_ (K. J. Hiscox, Entomologist. Butte County Mosquito Abatement Dist., pers. commun.). The fish did not reproduce and the study was terminated.

POECILIIDAE—livebearer family

16. _Gambusia affinis holbrooki_ Girard—eastern mosquitofish

The eastern mosquitofish has been widely distributed in the public waters of California by various mosquito abatement districts

(E. F. Legner and K. J. Hiscox, pers. commun.). It is believed to be more tolerant of colder temperatures than the western mosquitofish. The two subspecies hybridize readily and collections of pure *G. a. holbrooki* have yet to be made in the wild.

17. *Lebistes reticulatus* (Peters)—guppy

Besides the almost certain release of guppies by tropical fish fanciers, guppies have been stocked on numerous occasions in wastewater treatment ponds scattered around the State where access to public waters is possible (K. J. Hiscox, pers. commun.). In 1968 the Fish and Game Commission approved a request by the University of California, Riverside, to stock guppies in dairy and poultry waste lagoons in San Bernardino County (E. C. Bay, pers. commun.). Also in 1968, the Commission permitted the Kings Mosquito Abatement District to release guppies in lower Mill Creek in Tulare and Kings counties. None of the foregoing introductions led to the establishment of permanent populations. However, wild populations can be anticipated in suitable areas with year-round warmwater temperatures.

18. *Rivulus hartii* (Boulenger)—Trinidad rivulus

St. Amant (1970) first observed and collected this species in a small ditch near a tropical fish farm in Imperial County in 1967. It was identified by C. L. Hubbs. Additional specimens were collected in 1968. Both adults and juveniles were taken in 1969. The population has since disappeared.

19. *Xiphophorus variatus* (Meek)—variable platyfish

St. Amant and Sharp (1971) collected approximately 200 adult and juvenile *Xiphophorus variatus*, a native of Mexico, from a drain ditch 6.4 km (4 miles) east of Oasis, Riverside County on 24 December 1969. This was the first record of an established population. C. L. Hubbs confirmed the identification. They have since died out.

ATHERINIDAE—silverside family

20. Labidesthes sicculus (Cope)—brook silverside

The brook silverside was one of five species authorized by the Fish and Game Commission in 1963-64 for introduction into experimental ponds beside Clear Lake. These ponds, plus a deep well, were constructed in 1963 by the Lake County Mosquito Abatement District "for the express purpose of evaluating experimental fishes and their influence on biological productivity" (Cook 1968). The Labidesthes, obtained from Ohio, did well in one pond for 3 years and reproduced, but then died out from unknown causes.

CENTRARCHIDAE—sunfish family[3/]

21. Ambloplites rupestris (Rafinesque)—rock bass

21a. Ambloplites rupestris rupestris (Rafinesque)—northern rock bass

It is recorded in literature as having been introduced in 1874 and again in 1891, and another record of a plant of "rock bass" in 1917 was furnished by E. H. Glidden. Brief statements by Neale

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[3/] "Lepomis euryorus McKay". Seale (1930) lists "Sunfish, Eupomotis euryoris" in an article entitled, "List of twenty fresh water fishes found in California that may be used in small aquariums or garden pools." The Steinhart Aquarium accession list for 1931 records "Apomotis euryorus" as collected near Willows, California. The identification was made by Alvin Seale; the specimens were not saved. Hubbs and Hubbs (1932) have proved that the nominal species "Lepomis euryorus" is a hybrid between Lepomis cyanellus and Lepomis gibbosus. Both of these species are known to be present in California but L. gibbosus has not yet been recorded from near Willows, nor do we have any records of its presence in the State as early as 1930 or 1931.

(1931) and Anon. (1934) as to its limited success in California, and its occasional listing in State fish rescue records up to 1939, are the only bases for belief that this fish ever endured. The terminology used in these rescue records (published in the Biennial Reports of the California Division of Fish and Game) has often been inexact. We have been unable to find a single verifiable record of the occurrence of the rock bass in California.

22. Ennaecanthus gloriosus (Holbrook)—bluespotted sunfish

This species is listed in the accession list for Steinhart Aquarium as having been collected in March 1931 in the vicinity of Willows, California. The identification was made by Alvin Seale, but the specimens were not saved. We believe this to be a misidentification.

23. Lepomis macrochirus Rafinesque—bluegill

23a. Lepomis macrochirus speciosus (Baird and Girard)—southwestern bluegill

According to Miller (1952), "The southwestern bluegill...is also now evidently established in the Colorado River through introduction...(fide C. L. Hubbs in letter of 10 May 1951, to R. D. Beland, and letter from Beland of 23 August 1951 to W. A. Dill)."

PERCIDAE—perch family

24. Stizostedion vitreum (Mitchill)—walleye

Miller (1967) summarized the history of walleye introductions in California. The first introduction occurred in 1874 when 16 fish from the Missiquoi River in Vermont were stocked in the Sacramento River near Sacramento. One was caught by an angler but nothing further was recorded from the plant.

The second attempt spanned the years 1959 to 1963, when the California Department of Fish and Game, through the cooperation of the Minnesota Conservation Department, secured large numbers of eggs from walleye captured in the Detroit River, Minnesota. About 5,350,000 fry and 34,590 fingerlings were stocked in five southern California warmwater reservoirs in 1959, 1960, 1962, and 1963. These plants were successful in that good survival and growth was experienced, however, anticipated angling benefits did not accrue and the program was abandoned. Natural spawning did not take place and the original plants gradually died out.

CICHLIDAE—cichlid family

25. Cichlasoma beani (Jordan)—green guapote

A well-established population of this species was discovered in 1975 in several small ponds adjacent to Putah Creek in Solano County by Al Castro, Aquarist with the California Academy of Sciences (pers. commun.). Identification was made by W. I. Follett. Sampling in 1979 did not uncover any specimens and some of the ponds were dry, so apparently the species did not survive (R. L. Reavis, Fishery Biologist, Calif. Dep. Fish and Game, pers. commun.).

REFERENCES

Anon. 1934. The rock bass (Ambloplites rupestris). Aquarium J. 7(10): 192.

____. 1958. The Salton Sea story. Outdoor Calif. 19(12):4-7, 13.

Bailey, R. M. 1956. A revised list of the fishes of Iowa with keys for identification. Pages 327-377 in Iowa Fish and Fishing (Third edition). Iowa St. Cons. Comm.

Bailey, R. M., and C. E. Bond. 1963. Four new species of freshwater sculpins, genus Cottus, from western North America. Univ. Mich Mus. Zool. Occ. Papers no. 634. 27 p.

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada (Third edition). Amer. Fish. Soc., Special Publ. 6. 150 p.

Bailey, R. M., and T. Uyeno. 1964. Nomenclature of the blue chub and the tui chub, cyprinid fishes from western United States. Copeia 1964(1):238-239.

Bailey, R. M., H. E. Winn, and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecological and taxonomic notes. Proc. Acad. Nat. Sci. Phila. (106):109-164.

Bay, E. C. 1966. Adaptation studies with the Argentine pearl fish, Cynolebias bellottii, for its introduction into California. Copeia 1966(4):839-846.

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. Can., Fish. Res. Bd., J. 29(6):639-671.

Benson, S. B., and R. J. Behnke. 1961. Salmo evermanni a synonym of Salmo clarkii henshawi. Calif. Fish Game 47(3):257-259.

Bills, F. T., and C. E. Bond. 1980. A new subspecies of tui chub (Pisces: Cyprinidae) from Cowhead Lake, California. Copeia 1980(2): 320-322.

Black, G. F. 1980. Status of the desert pupfish Cyprinodon macularius (Baird and Girard), in California. Calif. Dep. Fish and Game, Inland Fish. Endangered Species Program, Special Publ. 80-1. 42 p.

Bond, C. E. 1961. Keys to Oregon freshwater fishes. Agr. Expt. Sta. Oregon St. Univ. Tech. Bull. 58. 42 p.

__________. 1973. Occurrence of the reticulate sculpin, Cottus perplexus, in California, with distributional notes on Cottus gulosus in Oregon and Washington. Calif. Fish Game 59(1):93-94.

Bottroff, L. J., and M. E. Lembeck. 1978. Fishery trends in reservoirs of San Diego County, California, following the introduction of Florida largemouth bass, Micropterus salmoides floridanus. Calif. Fish Game 64(1):4-23.

Bottroff, L. J., J. A. St. Amant, and W. Parker. 1969. Addition of Pylodictis olivaris to the Californian fauna. Calif. Fish Game 55(1):90.

Brittan, M. R., A. B. Albrecht, and J. B. Hopkirk. 1963. An oriental goby collected in the San Joaquin River Delta near Stockton, California. Calif. Fish Game 49(4):302-304.

Brittan, M. R., J. D. Hopkirk, J. D. Conners, and M. Martin. 1970 Explosive spread of the oriental goby Acanthogobius flavimanus in the San Francisco Bay-Delta region of California. Proc. Calif. Acad. Sci. 38(11):207-214.

Brown, D., K. D. Aasen, and C. E. von Geldern, Jr. 1977. Alabama spotted bass grow at record rate in Lake Perris, California. Calif. Fish Game 63(1):60-64.

California Department of Fish and Game. 1978. At the crossroads, 1978, a report on California's endangered and rare fish and wildlife. Calif. Dep. Fish and Game x + 103 p.

Cavender, T. M. 1978. Taxonomy and distribution of the bull trout, Salvelinus confluentus (Suckley), from the American northwest Calif. Fish Game 64(3):137-174.

Coates, C. W. 1942. Tropical fishes for a private aquarium. Cleveland and New York, the World Publ. Co., xi + 226 p.

Coleman, G. A. 1930. A biological survey of Clear Lake, Lake County. Calif. Fish Game 16(3):221-227.

Colorado River Wildlife Council. 1977. Endemic species of the Colorado River system, a status report. Colorado River Wildl. Council, Endemic Species Committee. 16 p.

Cook, S. F., Jr. 1968. The potential role of fishery management in the reduction of chaoborid midge populations and water quality enhancements. Calif. Vector News 15(7):63-70.

Cook, S. F., Jr., and R. L. Moore. 1970. Mississippi silversides, Menidia audens (Atherinidae), established in California. Amer. Fish. Soc., Trans. 99(1):70-73.

Cook, S. F., Jr., R. L. Moore, and J. D. Conners. 1966. The status of the native fishes of Clear Lake, Lake County, California. The Wasmann J. Biol. 24(1):141-160.

Frantz, T. C., and A. J. Cordone. 1965. Introduction of the Bonneville cisco (Prosopium gemmiferum Snyder) in Lake Tahoe, California and Nevada. Calif. Fish Game 51(4):270-275.

________________. 1967. Final introductions of the Bonneville cisco (Prosopium gemmiferum Snyder) into Lake Tahoe. California and Nevada. Calif. Fish Game 53(3):209-210.

Girard, C. 1860. Ichthyological notices. Proc. Acad. Nat. Sci. Phila. (1859):157-161.

Gold, J. R., G.A.E. Gall, and S. J. Nicola. 1978. Taxonomy of the Colorado cutthroat trout (Salmo clarki pleuriticus) of the Williamson Lakes, California. Calif. Fish Game 64(2):98-103.

Goodson. L. F., Jr. 1966. Redeye bass. Pages 371-373 in A. Calhoun, ed., Inland Fisheries Management. Calif. Dep. Fish and Game. 546 p.

Grinnell, J., and A. H. Miller. 1944. The distribution of the birds of California. Cooper Ornith. Club, Pac. Coast Avifauna, no. 27. 608 p.

Hart, J. S. 1952. Geographic variations of some physiological and morphological characters in certain freshwater fish. Univ. Toronto Pr., Univ. Toronto Biol. Ser. no. 60, Publ. Ontario Fish. Res. Lab. no 72. 79 p.

Henry, F. D., Jr. 1979. The introduction of southeastern bluegill, Lepomis macrochirus purpurescens, into Lake Perris, California, with notes on the growth of the initial year class. Calif. Fish Game 65(4):279-281. (The identical article was published in 1980 Calif. Fish Game 66(1):62-64.)

Hoover, F. G., and J. A. St. Amant. 1970. Establishment of Tilapia mossambica Peters in Bard Valley, Imperial County, California. Calif. Fish Game 56(1):70-71

Hopkirk, J. D. 1973. Endemism in fishes of the Clear Lake region of central California. Univ. Calif. Publ. Zool. (96):135.

Hubbs, Carl L. 1967. Occurrence of the Pacific lamprey, Entosphenus tridentatus, off Baja California and in streams of southern California; with remarks on its nomenclature. Trans., San Diego Soc. Nat. Hist. 14(21):301-312.

____________. 1971. Lampetra (Entosphenus) lethophaga, new species, the nonparasitic derivative of the Pacific lamprey. Trans., San Diego Soc. Nat. Hist. 16(6):125-163.

Hubbs, C. L., W. I. Follett, and L. J. Dempster. 1979. List of the fishes of California. Calif. Acad. Sci. Occ. Papers no. 133. 51 p.

Hubbs, C. L., and L. C. Hubbs. 1932. Experimental certification of natural hybridization between distinct genera of sunfishes. Papers Mich. Acad. Sci. Arts and Let. 1931(15):427-437.

Hubbs, C. L., and R. R. Miller. 1948. The zoological evidence: correlation between fish distribution and hydrographic history in the desert basins of western United States. Pages 17-166 in The Great Basin, with emphasis on glacial and postglacial times. Bull. Univ. Utah 38(20), Biol. Ser. 10(7):191.

______________________________. 1965. Studies of cyprinodont fishes XXII. Variation in Lucania parva, its establishment in western United States, and description of a new species from an interior basin in Coahuila, Mexico. Misc. Publ. Mus. Zool, Univ. Mich, no. 127. 104 p.

Kimsey, J. B. 1954. The introduction of the redeye black bass and the threadfin shad into California. Calif. Fish Game 40(2):203-204.

____________. 1957. The status of the redeye bass in California. Calif. Fish Game 43(1):99-100.

Kimsey, J. B., and L. O. Fisk. 1960. Keys to the freshwater and anadromous fishes of California. Calif. Fish Game 46(4):453-479.

Kliukanov, V. A. 1970. Classification of smelts (Osmeridae) with respect to peculiarities of skeleton structure in the genus Thaleichthys. Zool. J. 49(3):399-417. (in Russian with English summary).

Knaggs, E. H. 1977. Status of the genus Tilapia in California's estuarine and marine waters. Cal-Neva Wildl. (1977):60-67.

LaBounty, J. F., and J. E. Deacon. 1972. Cyprinodon milleri, a new species of pupfish (family Cyprinodontidae) from Death Valley, California. Copeia 1972(4):769-780.

Lambert, T. R. 1980. Redeye bass, Micropterus coosae, in the South Fork Stanislaus River, California. Calif. Fish Game (in press).

La Rivers, I. 1962. Fishes and fisheries of Nevada. Nev. St. Fish and Game Comm., Carson City. 782 p.

Lindberg, G. U., and M. I. Lepeza. 1965. Fishes of the Sea of Japan and the adjacent areas of the Sea of Okhotsk and the Yellow Sea. Part 2, Teleostomi, XII. Acipenseriformes-XXVIII. Polynemiformes. Keys to Fauna USSR, Zool. Inst. Acad. Sci. USSR. no. 84. 391 p. Israel translation, 1969. viii + 389 p.

Mearns, A. J. 1975. Poeciliopsis gracilis (Heckel), a newly introduced poeciliid fish in California. Calif. Fish Game 61(4):251-253.

Meinz, M., and W. L. Mecum. 1977. A range extension for Mississippi silversides in California. Calif. Fish Game 63(4):277-278.

McAllister, D. E. 1963. A revision of the smelt family, Osmeridae. Nat. Mus. Can., Bull. 191. 53 p.

McCoid, M. J., and J. A. St. Amant. 1980. Notes on the establishment of the rainwater killifish, Lucania parva, in California. Calif. Fish Game 66(2):125-126.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Bull. (157):235.

Miller, L. W. 1967. The introduction, growth, diet, and depth distribution of walleye, Stizosteidion vitreum (Mitchell), in El Capitan Reservoir, San Diego County. Calif. Dep. Fish and Game, Inland Fish Admin. Rep. 67-10. 14 p.

Miller, R. R. 1952. Bait fishes of the lower Colorado River from Lake Mead, Nevada, to Yuma, Arizona, with a key for their identification. Calif. Fish Game 38(1):7-42.

___________. 1958. Origin and affinities of the freshwater fish fauna of western North America. Pages 187-222 in C. L. Hubbs ed., Zoogeography. Amer. Assoc. Adv. Sci. Publ. 51.

___________. 1963. Synonymy, characters, and variation of Gila crassicauda, a rare Californian minnow, with an account of its hybridization with Lavinia exilicauda. Calif. Fish Game 49(1):20-29.

___________. 1973. Two new fishes, Gila bicolor snyderi and Catostomus fumeiventris, from the Owens River basin, California. Univ. Mich. Mus. Zool. Occ. Papers no. 667. 19 p.

Minckley, W. L. 1973. Fishes of Arizona. Ariz. Game and Fish Dep., xv + 293 p.

Minckley, W. L., and J. E. Deacon. 1968. Southwestern fishes and the enigma of "endangered species". Science 159(3822):1424-1432.

Morton, W. M. 1970. On the validity of all subspecific descriptions of North American Salvelinus malma (Walbaum). Copeia 1970(3): 581-587.

Naiman, R. J., and E. P. Pister. 1974. Occurrence of the tiger barb, Barbus tetrazona, in the Owens Valley, California. Calif. Fish Game 60(2):100-101.

Norden, C. R. 1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (Thymallus articus) and its phylogeny. Can., Fish. Res. Bd., J. 18(5):679-791.

Richardson, W. M., J. A. St. Amant, L. J. Bottroff, and W. L. Parker. 1970. Introduction of blue catfish into California. Calif. Fish Game 56(4):311-312.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada (Fourth Edition). Amer. Fish. Soc., Special Publ. no. 12.

Rosen, D. E., and R. M. Bailey. 1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography and systematics. Bull. Amer. Mus. Nat. Hist. 126(1):1-176.

Ross, S. T. 1973. The systematics of Gasterosteus aculeatus (Pisces: Gasterosteidae) in central and southern California. Los Angeles County Nat. Hist. Mus. Contrib. Sci. no. 243. 20 p.

St. Amant, J. A. 1966. Addition of Tilapia mossambica Peters in the California fauna. Calif. Fish Game 52(1):54-55.

________________. 1970. Addition of Hart's rivulus, Rivulus harti (Boulenger), to the Californian fauna. Calif. Fish Game 56(2): 138.

St. Amant, J. A., and F. G. Hoover. 1969. Addition of Misgurnus anguillicaudatus (Cantor) to the Californian fauna. Calif. Fish Game 55(4):330-331.

St. Amant, J. A., and I. Sharp. 1971. Addition of Xiphophorus variatus (Meek), to the California fauna. Calif. Fish Game 57(2):128-129.

Sasaki, S. 1961. Introduction of Florida largemouth bass into San Diego County. Calif. Dep. Fish and Game, Inland Fish. Admin. Rep. 61-11. 6 p.

Seale, A. 1930. List of twenty fresh water fishes found in California that may be used in small aquariums or garden pools. Aquarium J. 3(7):38-39.

Schultz, L. P. 1957. The frogfishes of the family Antennariidae. Proc. U. S. Nat. Mus. 107(3383):47-105.

Shapovalov, L., and W. A. Dill. 1950. A check list of the fresh-water and anadromous fishes of California. Calif. Fish Game 36(4): 382-391.

Shapovalov, L., W. A. Dill, and A. J. Cordone. 1959. A revised check list of the freshwater and anadromous fishes of California. Calif. Fish Game 45(3):159-180.

Skinner, J. E. 1971. Anguilla recorded from California. Calif. Fish Game 57(1):76-79.

Smith, G. R. 1966. Distribution and evolution of the North American catostomid fishes of the subgenus Pantosteus, genus Catostomus. Misc. Publ. Mus. Zool., Univ. Mich. no. 129. 132 p.

Snyder, J. O. 1914. A new species of trout from Lake Tahoe. Bull. U. S. Bur. Fish. Dep. Commerce 32(1912):23-28.

____________. 1918. The fishes of the Lahontan system of Nevada and northeastern California. Bull. U. S. Bur. Fish. Dep. Commerce 35(1915-1916):31-86.

____________. 1935. California fresh water fish. Aquarium J. 8(9):146.

Stevenson, M. M. 1971. Percina macrolepida (Pisces, Percidae, Etheostomatinea), a new percid fish of the subgenus Percina from Texas. Southwestern Nat. 16(1):65-83.

Sturgess, J. A. 1976. Taxonomic status of Percina in California. Calif. Fish Game 62(1):79-81.

Svetovidov, A. N. 1952. Fishes: Clupeidae, 2(1):1-428 in Fauna of USSR, Zool. Inst. Akad. Nauk. SSSR ms 48 (English translation, 1963. Nat. Sci. Found., Wash., D.C.).

Taylor, T. L. 1980. A blue catfish from the Sacramento-San Joaquin Delta. Calif. Fish Game 66(2):120-121.

Taylor, W. R. 1954. Records of fishes in the John N. Lowe collection from the Upper Peninsula of Michigan. Misc. Publ. Mus. Zool., Univ. Mich. no. 87. 50 p.

Vandermeer, J. H. 1966. Statistical analysis of geographic variation of the fathead minnow, Pimephales promelas. Copeia 1966(3):457-466.

Vladykov, V. D. 1973. Lampetra pacifica, a new nonparasitic species of lamprey (Petromyzontidae) from Oregon and California. Can., Fish. Res. Bd., J. 30(2):205-213.

Vladykov, V. D., and W. I. Follett. 1965. Lampetra richardsoni, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. Can., Fish. Res. Bd., J. 22(1):139-158.

Vladykov, V. D., and E. Kott. 1976a. A new nonparasitic species of lamprey of the genus Entosphenus Gill, 1862, (Petromyzonidae) from south central California. Bull. So. Calif. Acad. Sci. 75(2):60-67.

______________________. 1976b. A second nonparasitic species of Entosphenus Gill, 1862 (Petromyzonidae) from Klamath River system, California. Can. J. Zool. 54(6):974-989.

von Geldern, C. E., Jr. 1966. The introduction of white bass (Roccus chrysops) into California. Calif. Fish Game 52(4):305.

Wales, J. H. 1962. Introduction of pond smelt from Japan into California. Calif. Fish Game 48(2):141-142.

Walker, B. W., R. R. Whitney, and G. W. Barlow. 1961. The fishes of the Salton Sea. Pages 77-92 in B. W. Walker ed., The ecology of the Salton Sea, California, in relation to the sportfishery. Calif. Dep. Fish Game, Fish Bull., (113):204.

CHECK LIST OF ARIZONA FISHES
by Bud Bassett

Salmonidae

Rainbow trout	Salmo gairdneri
Cutthroat trout	Salmo clarki
Gila native trout	Salmo gila
Brown trout	Salmo trutta
Brook trout	Salvelinus fontinalis
*Kokanee salmon	Onchorhynchus nerka kennerlyi
*Grayling	Thymallus signifer

Centrarchidae

Largemouth black bass	Micropterus salmoides
Smallmouth black bass	Micropterus dolomieui
Rock bass	Ambloplites rupestris
Bluegill	Lepomis macrochirus
Green sunfish	Lepomis cyanellus
Redear sunfish	Lepomis microlophus
White crappie	Poxomis annularis
Black crappie	Poxomis nigromaculatus
Warmouth	Chaenobryttus gulosus

Ictaluridae

Channel catfish	Ictalurus punctatus
Flathead catfish	Pylodictis olivaris
Blue catfish	Ictalurus furcatus
Black bullhead	Ameiurus melas
Yellow bullhead	Ameiurus natalis

Serranidae

*White bass	Roccus chrysops
Yellow bass	Roccus mississippiensis
Striped bass	Roccus saxatilis

Percidae

Yellow perch	Perca flavescens
*Walleye pike	Stizostedion vitreum

Cichlidae

Tilapia	Tilapia mossambica

Elopidae

Tenpounder	Elops affinis

Mugilidae

Striped mullet	Mugil cephalus

Clupeidae

Threadfin shad	Dorosoma petenense

Cyprinodontidae

Zebra minnow	Fundulus zebrinus
Desert pupfish	Cyprinodon maculanius

Catostomidae

Western white sucker	Catostomus commersoni
Gila sucker	Catostomus insignis
Yaqui coarsescale sucker	Catostomus bernardini
Lower Colorado Flannelmouth sucker	Catostomus latipinnis latipinnis
Bluehead mountain sucker	Pantosteus delphinus
Gila mountain sucker	Pantosteus clarki
Humpback sucker	Xyrauchen texanus
Smallmouth buffalofish	Ictiobus bubalus
Largemouth buffalofish	Ictiobus cyprinellus

Cyprinidae

Carp	Cyprinus carpio
Goldfish	Carassius auratus
Yaqui chubminnow	Gila purpurea
Sonora chub	Gila ditaenia
Roundtail chub	Gila robusta robusta
Small fin Colorado chub	Gila robusta intermedia
Intermediate Colorado chub	Gila robusta seminuda
Bonytail	Gila robusta elegans
Humpback chub	Gila cypha
Plains red shiner	Notropis lutrensis
Yaqui shiner	Notropis mearnsi
Western dace	Rhinichthys osculus
Longfin dace	Agosia chrysogaster
Fathead minnow	Pimephales promelas
Western golden shiner	Notemigonus crysolucas
Spikedace	Meda fulgida
Barbelled (wound fin)	Plagopterus argentissimus
Scaled spinedace	Lepidomeda vittata
Loach minnow	Tiaroga cobitus
Ornate stoneroller	Campostoma ornatum
Colorado River squawfish	Ptychocoheilus lucius
Virgin River spinedace	Lepidomeda mollispinis mollispinis
Utah chub	Gila atraria

Poecilidae

Mosquito fish	Gambusia affinis

* transient

KEYS FOR THE IDENTIFICATION OF THE FISHES IN ARIZONA

By Robert R. Miller
Museum of Zoology, University of Michigan
July, 1949

ARTIFICIAL KEY TO THE FAMILIES

1a. Adipose fin present 2

2a. Body scaleless; pectoral fin with a spine; barbels on lower jaw and posterior nostrils . . . . AMEIURIDAE (Catfishes)

2b. Body with small scales; no pectoral spine; no barbels . . . . SALMONIDAE (Trouts)

1b. Adipose fin absent 3

3a. Pelvic fins each with a well-developed, sharp spine and 5 soft rays, typically thoracic; two dorsal fins (united or separated) consisting of a spinous and a soft portion 4

4a. Anal spines 1 or 2 . . . . PERCIDAE (Yellow perch - <u>Perca flavescens</u>)

4b. Anal spines 3 or more (2 in young mullet) 5

5a. Dorsal spines widely separated, both small; not more than 4 spines in first dorsal; scales cycloid . . . . MUGILIDAE (Striped mullet - <u>Mugil cephalus</u>)

5b. Dorsal fins narrowly separated or united, conspicuously more than 4 spines in first dorsal; scales ctenoid . . . 6

6a. Pseudobranchiae well-developed, exposed; anal spines 3; 2 separate dorsal fins (weakly united at base in <u>Morone</u>) . . . . SERRANIDAE (Yellow base - <u>Morone interrupta</u>)

6b. Pseudobranchiae small and concealed by a membrane; anal spines 3 or more; dorsal fin single (almost separated in <u>Micropterus</u> salmoides) . . . CENTRARCHIDAE (Sunfishes)

3b. Pelvic fins without sharp spines and with more than 5 soft rays, abdominal; a single soft dorsal fin (with a spinous ray in carp, <u>Cyprinus carpio</u>, and goldfish, <u>Carassius auratus</u> 7

7a. Head completely scaleless; mouth terminal to inferior not transverse 8

8a. Bony gular plate present between branches of lower jaw; a prominent adipose eyelid . . . . ELOPIDAE
(Tenpounder - Elops affins)

8b. No gular plate; adipose eyelid absent 9

9a. Pharyngeal arch with a single, comb-like row of more than 25 teeth; anal fin posterior distance from its origin to middle of caudal base usually less than one-half the distance from anal origin forward to back of head. Mouth usually inferior, with thick fleshy papillose lips, caudal rays 18 . . . . CATOSTOMIDAE
(Suckers)

9b. Pharyngeal arch with one to three short rows of distinct teeth, the principal row with not more than 8 teeth; anal more anterior, distance from its origin to middle of caudal base usually more than one-half the distance forward to head. Mouth variable in position but with the lips typically thin (rarely somewhat fleshy but papillose). Caudal rays 19 . . . . CYPRINIDAE
(Minnows)

7b. Head partly scaled; mouth superior, transverse 10

10a. Anal fin in mature male not modified to form a spike-like gonopodium (specialized intromittent organ). Adults with anterior 1 or 2 anal rays unbranched. Adult female with the anterior anal rays sheathed at base by membranous fold . . . .
CYPRINODONTIDAE
(Desert pupfish - Cyprinodon maculanius)

10b. Anal fin in mature male with the third to fifth rays elongated to form a spike-like gonopodium. Adults with anterior 3 anal rays unbranched. Adult female with the anterior anal rays not sheathed at base . . . .
POECILIDAE
(Top minnows)

FAMILY AMEIURIDAE, Catfishes.

1a. Caudal fin deeply to slightly forked . . . . . . Ictalurus 2

2a. Length of anal fin base less than head length; anterior part of anal conspicuously higher than posterior portion; no spots developed on body. (Recorded once from headwaters of Yaqui River; introduced into Monkey Spring). Ictalurus pricei (Pacific channel cat)

2b. Length of anal fin base longer than head length; anal fin rather uniform in height throughout; spots and flecks developed on body (particularly in half-grown) . . . Ictalurus lacustris lacustris * (Common channel cat)

1b. Caudal fin weakly emarginate to rounded . . . . . Ameiurus 3

3a. Anal rays 24 to 27 (including minute rudiments); caudal fin rounded; mental barbels whitish; no whitish bar at caudal base. Ameiurus natalis* (Yellow bullhead)

3b. Anal rays 17 to 21 (including rudiments); caudal fin evidently emarginate; mental barbels to grey to black; fine with jet-black membranes; adults with whitish bar at caudal base. Ameiurus melas* (Black bullhead)

FAMILY POECILIDAE. Topminnows

1a. Dorsal origin well behind anal origin (applicable to females only), composed of six rays (last 2 counted as 1); no dark lateral streak, teeth sharply conical, arranged in a single arc following outline of jaws. . . . . Gambusia affinis affinis* (Western mosquitofish)

1b. Dorsal origin only slightly behind anal origin (applicable to females only); composed of 7 rays (last 2 counted as 1); prominent dark lateral streak; teeth spatulate, arranged in 2 equal arcs (sloping inward at apex) in each jaw . . . . . . Poeciliopsis occidentalis (Gila topminnow)

FAMILY CENTRARCHIDAE. Sunfishes

1a. Anal spines 3 (rarely 2 or 4) 2

2a. Body elongate; lateral line scales 55 or more. Micropterus salmoides* (Largemouth bass)

2b. Body deep, compressed; lateral line scales less than 55; no teeth on tongue . . . . Lepomis 3

3a. Opercle stiff to its margin; mouth large; pectoral fins short and rounded, contained about 4 times in standard length . . . . Lepomis cyanellus* (Green sunfish) . . .

3b. Opercle produced into a thin, flexible projection; mouth small; pectoral fins long and pointed contained about 3 times in standard length . . . . Lepomis macrochirus 4

4a. Anal soft rays 10 to 12, usually 11 . . . . Lepomis macrochirus macrochirus . . . . (Common bluegill)

4b. Anal soft rays 9 to 11, usually 10 . . . . Lepomis macrochirus speciosus* (Southwestern bluegill)

1b. Anal spines 5 or more 5

5a. Dorsal spines normally 7 or 8; length of dorsal fin base about equal to distance from origin of dorsal to eye Pomoxis nigro-maculatus* (Black crappie)

5b. Dorsal spines normally 6; length of dorsal fin base much less than distance from origin of dorsal to eye Pomoxis annularis* (White crappie)

ARTIFICIAL KEY TO GENERA, SPECIES, AND SUBSPECIES

Since Cyprinodon macularius (Cyprinodontidae), Perca flavescens* (Percidae), Morone interrupta* (Serranidae), Mugil cephalus (Mugilidae), and Elops affinis (Elopidae) are the only representative of their respective families, they may be identified by using the family key. Introduced species are marked by an asterisk.

FAMILY SALMONIDAE. Trouts

1a. Vomer flat, the shaft not depressed, bearing a zig-zag row or alternating rows of teeth; species with black or brown spots (reddish spots in the brown trout) . . . . Salmo 2

2a. Cutthroat mark (between branches of lower jaw) conspicuous in life, usually blood-red in adults (varying from yellow-orange salmon); hyoid teeth present; scales along side just above lateral line more than 155; tips of pelvic and anal fins without light border rosy, dusky, or plain in life . . . .
Salmo clarkii lewisi* (1)
(Yellow stone cutthroat trout)

2b. Cutthroat mark absent; no hyoid teeth; scales along side just above lateral line fewer than 140; tips or margins of pelvic and anal fins with a light border, milky-white or yellowish in life 3

3a. Black or brown spots larger and more diffuse, scarcely developed on caudal fin; reddish spots more or less strongly developed; adipose fins of young orange, without dark margin or spots; pectoral fin larger and heavier.
. . . . Salmo trutta fario
(Brown trout)

3b. Black or (brown spots) smaller and sharper, well-developed on caudal fin; red spots never developed; adipose fin of young olive, with black margin or spots; pectoral fin shorter
Salmo gairdnerii irideus*
(Rainbow trout)

1b. Vomer with trough-like, toothless shaft, the teeth confined to the head of the bone; species spotted with red or yellow . . . .
Salvelinus fontinalis* (Brook trout)

(1) The Colorado cutthroat trout, Salmo clarkii pleuriticus, once inhabited upper tributaries of Little Colorado River on the north slope of the White Mountains. This subspecies is now believed to be extinct in Arizona.

FAMILY CATOSTOMIDAE. Suckers.

1a. Predorsal region between occiput and dorsal fin with a razor-like ridge . . . . <u>Xyrauchen texanus</u> (Razorback sucker)

1b. Predorsal region without a compressed, elevated ridge 2

2a. A distinct notch at corner of mouth between upper and lower lips; upper lip recurved, smooth; lower lip little incised; edge of jaw inside lower lip with a hard, cartilaginous sheath . . . 3 <u>Pantosteus</u>

3a. Scales along lateral line 65 to 80; predorsal scales especially large, 19 to 25 . . . . <u>Pantosteus clarkii</u> (Gila mountain sucker)

3b. Scales along lateral line 82 to 105; predorsal scales smaller, 30 to 55 . . . . <u>Pantosteus delphinus</u> (Colorado mountain sucker)

2b. No distinct notch at corner of mouth between upper and lower lips; upper lip nearly flat; papillose; edge of jaw inside lower lip without a hard, cartilaginous sheath . . . . . <u>Catostomous</u> . . 4

4a. Scales along lateral line 89 to 102; caudal peduncle long and pencil-shaped; dorsal rays 13 to 15 . . . . <u>Catostomous latipinnis latipinnis</u> (Lower Colorado flannelmouth sucker)

4b. Scales along lateral line 55 to 73; caudal peduncle deep and heavy set; dorsal rays 10 to 12 . . . <u>Catostomous insignis</u> . 5 (Coarsemouth sucker)

5a. Snout longer, the preorbit and postorbital equal or subequal; body deeper anteriorly, its greatest depth more than that of the head length; scales averaging smaller, 63 to 73 . . . . <u>Catostomous bernardini</u> (Yaqui coarsescale sucker)

5b. Snout shorter, the preorbital and postorbital equal or subequal; body deeper anteriorly, its greatest depth more than that of the head length; scales averaging smaller, 63 to 73 . . . . <u>Catostomous bernardini</u> (Yaqui coarsescale sucker)

FAMILY CYPRINIDAE. Minnows

1a. Dorsal and anal fins each preceded by a serrated spine; dorsal fins elongate, of 17 or more soft rays 2

2a. Upper jaw with two fleshy barbels on each side; lateral line scales 35 to 38 (sometimes scaleless, Leather Carp, or partially scaled, Mirror Carp); gill rakers on first arch 21 to 27; pharyngeal teeth in 3 rows on each arch; 1, 1, 3-3, 1, 1. Introduced from Eurasia . . . . Cyprinus carpio* (Carp)

2b. Upper jaw without barbels; lateral line scales 26 to 29; gill rakers on first arch 37 to 43; pharyngeal teeth in a single row; 4-4. Introduced from Eurasia . . Carassius auratus* (Goldfish)

1b. Dorsal and anal fins not preceded by a serrated spine, the dorsal fin comprised of two smooth spines or none at all; dorsal fin short of 11 or fewer rays 3

3a. Dorsal fin preceded by 2 full-length spines, the anterior with a longitudinal groove on its posterior face to receive the posterior spine; most of pelvic rays spinose, the inner border of the pelvic fins attached to the body . . . . . . Plagopterinae 4

4a. Body essentially scaleless 5

5a. Maxillary with a barbel on each side of head; dental formula 2, 5-4, 2 or 2, 5-4, 1 . . Plagopterus argentissimus (Barbelled spiny dace)

5b. Maxillary without a barbel; dental formula 1, 4-4, 1 . . . . Meda fulgida (Scaleless spiny dace)

4b. Body scaled except behind pectoral fins; no barbel; dental formula 2, 4-4, 2 . . . . . Lepidomeda vittata (Scaled spiny dace)

3b. Dorsal fin composed of soft rays only; pelvic rays not spinose and pelvic fins not bound down to body 6

6a. Body elongate, pike-like; mouth large, horizontal; maxillary reaching front of pupil; lower limb of pharngeal arch extremely elongated . . . . . Ptychocoheilus lucius . . . . (Ptychocoheilus lucius (Colorado squawfish)

6b. Body not elongate or pike-like; the mouth not large and horizontal maxillary shorter, not reaching front or pupil; lower-limb of pharyngeal arch not greatly elongated 7

7a. Lower jaw with conspicuous horny sheath inside lips, intestine greatly elongated, thrown to many coils lying adjacent to air bladder . . . Campostoma ornatum (Ornate stoneroller)

7b. Lower jaw without a conspicuous horny sheath; intestine elongated to form coils lying adjacent to air bladder 8

8a. A broad frenum connecting upper lip with snout; gill openings extremely restricted; mouth small, subinferior, with fleshy lips . . . Tiaroga cobitis ..(Loach Minnow)

8b. Frenum absent (or, at most, a narrow bridge developed); gill openings not narrowly restricted; mouth various, but lacking fleshy lips 9

9a. Pharyngeal teeth in two rows 10

10a. A small maxillary barbel usually present; dental formula 2, 5-4, 2;or 1,4-4, 1; mouth small, inferior, anal rays 7 (very rarely 8). Rhinichthys osculus (Western dace)

10b. Barbels never developed; dental formula 2, 5-4, 2; mouth larger, usually terminal and oblique (but inferior in Gila cypha and G. ditaenia); anal rays are variable (7-11) Gila 11

11a. Scales moderate to rather small, well-developed, with numerous radii on all fields; 45-75 in lateral line 12

12a. Scales in lateral line. 52-60 Gila purpurea (Yaqui chubminnow)

12b. Scales in lateral line 63-75. Gila ditaenia (Sonora chub)

11b. Scales small, variable in development (almost wholly lacking in Gila robusta elegans and G. cypha), usually without basal radii (rather weak when present 65 to 96 in lateral line . . . 13

13a. Nape with, at most, a broad, even convexity; body fully scaled to largely naked (65 to 96 scales along lateral line); snout not fleshy; mouth terminal to subterminal; eye moderate to small . . . Gila robusta (Colorado river chub) 14

14a. Dorsal rays usually 8 (rarely 7 or 9); anal rays 8 (7-9); pelvic rays 8-8 (frequently 9-9): fully scaled, 65 to 87 in lateral line; basal radii usually present; least depth of caudal peduncle enters the head length 2.6 to 3.4 times . . Gila robusta intermedia (Small fin Colorado chub)

14b. Dorsal rays usually 9 (rarely 8 or 10); anal rays 0 (rarely 7, 8 or 10); pelvic rays 9-9 (rarely 10-10); fully scaled, 79 to 96 in lateral line basal radii infrequent; least depth of caudal peduncle enters the head length 3.3 to 4.3 times. Gila robusta robusta (River Colorado chub)

14c. Dorsal rays 9 or 10; anal rays 9 or 10; pelvic rays 9-9 or 10-10; back, breast, and belly naked in some; 77-89 scales in lateral line, 2 out of 5 with very faint basal radii; least depth of caudal peduncle enters the head length 4.1 to 5.2 times (Gila robusta seminuda (1) (Intermediate Colorado chub)

14d. Dorsal rays 10 to 11; anal rays 10 or 11; pelvic rays 9-9 (rarely 10-10); back, breast, and belly and much of caudal peduncle often naked or with minute, deeply-imbedded scales; 75-88 in lateral line; no basal radii; least depth of caudal peduncle enters the head length 5.0 to 6.5 times. . . Gila robusta elegans (Bonytail)

13b. Nape with prominent hump, truncate anteriorly; body almost entirely devoid of scales (about 80 along lateral line); snout fleshy; mouth inferior; eye very small . . . . Gila cypha (Humpback chub)

9b. Pharyngeal teeth uniserial 15

15a. Maxillary with a small barbel; scales small, 73-95 in lateral line, with radii on all fields; anal fin elongate. Agosia chyrsogaster (Longfin dace)

15b. Barbels absent; scales large, fewer than 40 in lateral line, no basal radii; anal fin not elongate . . . Notropis mearnsi (Yaqui shiner) . .

(1) Based on five type specimens in the U. S. National Museum.

GENERAL KEY TO THE CYPRINIDAE OF COLORADO
Using External Characters Only
H. A. Tanner

1. Dorsal fin elongate, more than 15 rays, first dorsal & anal ray spiny, serrate 2

   Dorsal fin not elongate, less than 12 rays, spines absent 3

2. Barbels present at each corner of mouth . . . . Cyprinus
   Barbels absent . . . . Carassius

3. Barbels present at corner of mouth (sometimes minute) 4
   Barbels absent 7

4. Barbel large, dorsal, anal and paired fins with rounded posterior Border . . . . Tinca
   Fins not all rounded as above 5

5. Black spot at base of Dorsal fin at origin, mouth large . . . . Semotilus

   Black spot at base of dorsal absent. Posterior edge of mouth not reaching orbit 6

6. Body blochy and spotted in color . . . . Rhynichthys
   Body color uniform - silvery in appearance . . . . Hybopsis

7. Scales in laterial line more than 55 8
   Scales in laterial line less than 53 10

8. Head pike like, flattened-large mouth . . . . Ptchocheilus
   Head not pike like, mouth small or moderate 9

9. Laterial line indistinct or wanting, two black laterial bands present . . . . Chrosomus

   Laterial line distinct, no black bands present, caudal peduncle typically narrow-basal fulcra enlarged . . . . Gila

10. Fleshy keel (unscaled) present between pelvics and anal fin . . . . Notemigonus

    Fleshy keel absent 11

11. Lower jaw with cartilaginous ridge. Separated from lip by definite grove . . . . Campostoma

    Cartilaginous ridge absent 12

12. Body stout "humpbacked" first dorsal ray short, stout, blunt in male . . . . <u>Pimephales</u>

Vertical dark band across rays of caudal fin, first dorsal ray not short, blunt, stout. Black spot absent 13

13. Small hard protuberence on tip of lower jaw. Dorsal fin rounded. Color in life brassy . . . . <u>Hybognathus</u>

Protuberence absent 14

14. Mouth sucker-like, fleshy upper lip connected to lower lip. Lower lip made up of two lateral lobes divided in middle by broad, horny frenum . . . . <u>Phenacobius</u>

Mouth normal, terminal and oblique . . . . <u>Notropis</u>

FISHES OF COLORADO

The following lists indicate the diversity of fishes in Colorado and provide a guide to the distribution of fish species by drainage. The major drainages of Colorado include the Colorado River, which drains the state west of the continental divide; the South Platte, which carries water northeast to Nebraska; the Republican River, with headwaters in eastern Colorado; the Arkansas River, which flows southwest into Kansas; and the Rio Grande, which flows through the San Luis Valley south to New Mexico. Colorado fishes may be designated as native, game, and threatened or endangered species.

Fishes native to a major drainages within the state are designated by the letter N following the common name of the species. Those species lacking this designation are non-native to that drainage. It is readily apparent that many species, in addition to those purposely introduced to provide sport fishing, have become established throughout Colorado. The Colorado Division of Wildlife recognizes a majority of the fish species present in the state as game fish. The game species are designated by the letter G. Those fish lacking this designation are either threatened, endangered, or are non-game species (meaning that they are not commonly sought for sport or profit). Remember that this is solely a classification for management purposes and does not imply that all species considered game fish are actively pursued by anglers.

Several of the fish native to Colorado have been classified as "threatened" or "endangered". Threatened or endangered status may be assigned to a species by either state or federal agencies. State classification is made by the Colorado Wildlife Commission. Federal listing of such species is done by the Secretary of the U.S. Department of the Interior. Threatened refers to any species or subspecies of wildlife which is not in immediate jeopardy of extinction but is vulnerable because it exists in such small numbers or is so restricted throughout all or a significant portion of its range that it may become endangered in the foreseeable future. Endangered refers to any species or subspecies of wildlife whose prospects of survival or recruitment are so limited that it is in immediate jeopardy of becoming extinct.

On the species lists, fishes classified as threatened or endangered will be designated as follows: threatened in Colorado - TC; endangered in Colorado - EC; threatened nationally - TN; and endangered nationally - EN. It should be noted that these classifications are subject to change depending on the success of recovery plans.

On the following lists, a species may have one or two symbols following its common name depending on whether it is native, a game species, or threatened or endangered in the state or nationally.

MAJOR DRAINAGES OF COLORADO

(1) not native

LIST OF COLORADO FISHES BY DRAINAGE SYSTEM

FAMILY	COLORADO	PLATTE	ARKANSAS	RIO GRANDE	REPUBLICAN
Anguillidae	—	old record —	American eel (N, G) *Anguilla rostrata*	—	—
Clupeidae	Gizzard shad (G) *Dorosoma cepedianum*	(1) Gizzard shad (N, G) *Dorosoma cepedianum*	Gizzard shad (G) *Dorosoma cepedianum*	—	—
Salmonidae	Coho (silver) salmon (G) *Oncorhynchus kisutch*	Cutthroat Trout (N, G) *Salmo clarki* stomias	Eastern Brook trout (G) *Salvelinus fontinalis*	Eastern Brook trout (G) *Salvelinus fontinalis*	Rainbow trout (G) *Salmo gairdneri*
	Sockeye (kokanee) salmon (G) *Oncorhynchus nerka*	Rainbow trout (G) *Salmo gairdneri*	Cutthroat trout (N, G) *Salmo clarki* ~~virginalis~~ stomias	Cutthroat trout (N, G) *Salmo clarki* virginalis	Brown trout (G) *Salmo trutta*
	Mountain Whitefish (N, G) *Prosopium williamsoni*	Brown trout (G) *Salmo trutta*	Rainbow trout (G) *Salmo gairdneri*	Rainbow trout (G) *Salmo gairdneri*	
g	Golden trout (G) *Salmo aguabonita*	Eastern Brook trout (G) *Salvelinus fontinalis*	Brown trout (G) *Salmo trutta*	Brown trout (G) *Salmo trutta*	
	Cutthroat trout (N, G) *Salmo clarki* pleuriticus	Arctic Grayling (G) *Thymallus arcticus*	source for stocking is Ark. basin		
	Rainbow trout (G) *Salmo gairdneri*	Mountain Whitefish (G) *Prosopium williamsoni*	Twin L. lake trout kokanee		
	Brown trout (G) *Salmo trutta*	Lake whitefish Cheeseman Res. Coregonus clupeaformis			
	Eastern Brook trout (G) *Salvelinus fontinalis*	lake trout kokanee			
	Lake trout (G) *Salvelinus namaycush*				
	Arctic Grayling (G) *Thymallus arcticus*				
Esocidae	Northern Pike (G) *Esox lucius*	Northern Pike (G) *Esox lucius*	—	Northern Pike (G) *Esox lucius*	—

FAMILY	COLORADO	PLATTE	ARKANSAS	RIO GRANDE	REPUBLICAN
Cyprinidae	Lake Chub (G) *Couesius plumbeus*	Goldfish (G) *Carassius auratus*	Longnose dace (N, G) *Rhinichthys cataractae*	Rio Grande Chub (N, G) *Gila pandora*	Common (European) Carp (G) *Cyprinus carpio*
	Common (European) Carp (G) *Cyprinus carpio*	Common (European) Carp (G) *Cyprinus carpio*	Stoneroller (N, G) *Campostoma anomalum*	Longnose dace (N, G) *Rhinichthys cataractae*	Goldfish (G) *Carassius auratus*
	prob. not in Colo. Utah Chub *Gila atraria*	Stoneroller (N, G) *Compostoma anomalum*	Red Shiner (N, G) *Notropis lutrensis*	Fathead Minnow (N, G) *Pimephales promelas*	Creek Chub (N, G) *Semotilus atromaculatus*
	Colo ? Leather side Chub *Gila copei*	extirpated Lake Chub (N, G) *Couesius plumbeus*	Sand Shiner (N, G) *Notropis stramineus*	Common (European) Carp (G) *Cyprinus carpio*	Suckermouth minnow (N, G) *Phenocobius mirabilis*
	Humpback Chub (N, EN) *Gila cypha*	Brassy Minnow (N, G) *Hybognathus hankinsoni*	Fathead Minnow (N,G) *Pimephales promelas*	Tench (N) *Tinca tinca*	River Shiner (N, G) *Notropis blennius*
	Bonytail Chub (N, EN) *Gila elegans*	Silvery Minnow (N) *Hybognathus nuchalis*	Suckermouth Minnow (N, G) *Phenacobius mirabilis*	Red Shiner (N, G) *Notropis lutrensis*	Sand Shiner (N, G) *Notropis stramineus*
	Roundtail Chub (N *Gila robusta*	Western Silvery Minnow (N) *Hybognathus orgyritis*	So. Redbelly Dace (N, G) *Chrosomus erythragaster*	Sand Shiner (N, G) *Notropis stramineus*	Red Shiner (N, G) *Notropis lutrensis*
	Brassy Minnow (G) *Hybognathus hankinoni*	Plains Minnow (N, G) *Hybognathus placitus*	Tench (G) *Tinca tinca*	Bluntnose Shiner (N) *Notropis simus*	Brassy Minnow (N, G) *Hybognathus hankinsoni*
	Red Shiner (G) *Notropis lutrensis*	Flathead Chub (N, G) *Hybopsis gracilis*	Flathead Chub (N, G) *Hybopsis gracilis*	Rio Grande Shiner (N) *Notropis jemezanus*	Plains Minnow (N, G) *Hybognathus placitus*
	Sand Shiner (G) *Notropis stramineus*	Hornyhead Chub (N, G) *Nocomis biguttatus*	Hornyhead Chub (N, G) *Nocomis biguttatus*		Stoneroller (N, G) *Campostoma anomalum*
	Fathead Minnow (G) *Pimephales promelas*	Golden Shiner *Notemigonus crysoleucas*	Arkansas River Shiner (N) *Notropis girardi*		Fathead Minnow (N, G) *Pimephales promelas*
	Colorado Squaw fish (N, EN) *Ptychocheilus lucius*	River Shiner (N, G) *Notropis blennius*	River Shiner (N, G) *Notropis blennius*		
	Longnose dace (G) *Rhinichthys cataractae*	Common Shiner (N, G) *Notropis cornutus*	Creek Chub (N, G) *Semotilus atromaculatus*		
	Speckled Dace (N, G) *Rhinichthys osculus*	Bigmouth Shiner (N, G) *Notropis dorsalis*	Common (European) Carp (G) *Cyprinus carpio*		
	Redside Shiner (G) *Richardsonius balteatus*	Blacknose Shiner (N, G) *Notropis heterolepis*	Arkansas River Speckled Chub (N, TC) *Hybopsis aestivalis tetranemus*		
	Creek Chub (G) *Semotilus atromaculatus*	Red Shiner (N, G) *Notropis lutrensis*	Common Shiner (N, G) *Notropis cornutus*		
		Sand Shiner (N, G) *Notropis stramineus*			

FAMILY	COLORADO	PLATTE	ARKANSAS	RIO GRANDE	REPUBLICAN
Cyprinidae (continued)		Mimic Shiner *Notropis volucellus*	Plains Minnow (N, G) *Hybognathus placitus*		
		Bleeding Shiner *Notropis zonatus*			
		Suckermouth Minnow (N, G) *Phenacobius mirabilis*			
		No. Redbelly dace (N, G) *Phoxinus eos*			
		So. Redbelly dace (N, G) *Phoxinus erythrogoster*			
		Fathead Minnow (N, G) *Pimephales promelas*			
		Longnose Dace (N, G) *Rhinichthys cataractae*			
		Creek Chub (N, G) *Semotilus atromaculatus*			
Catostomidae	Utah Sucker *Catostomus ardens*	Longnose Sucker (N, G) *Catostomus catostomus*	Longnose Sucker (N, G) *Catostomus catostomus*	White Sucker (N, G) *Catostomus commersoni*	White Sucker (N, G) *Catostomus commersoni*
	Longnose Sucker (G) *Catostomus catostomus*	White Sucker (N, G) *Catostomus commersoni*	White Sucker (N, G) *Catostomus commersoni*	Rio Grande Sucker (N, G) *Catostomus plebius*	
	White Sucker (G) *Catostomus commersoni*	Rio Grande Sucker (G) *Catostomus plebius*			
	Colorado (Bluehead) Sucker (N, G) *Catostomus discobolus*	Carpsucker (N, G) *Carpiodes carpio*			
	Flannelmouth Sucker (N, G) *Catostomus latipinnis*	Quillback (Plains) Carp-sucker (G) *Carpiodes cyprinus*			
	Mountain Sucker (N, G) *Catostomus platyrhynchus*	Northern Redhorse (G) *Moxostoma macrolepidotum*			
	Razorback Sucker (N, EC) *Xyrauchen texanus*				

FAMILY	COLORADO	PLATTE	ARKANSAS	RIO GRANDE	REPUBLICAN
Ictaluridae	Black bullhead (G) Ictalurus melas Channel Catfish (G) Ictalurus punctatus	Black bullhead (G) Ictalurus melas Brown bullhead (G) Ictalurus nebulosus Channel Catfish (N, G) Ictalurus punctatus Stonecat (N) Noturus flavus	Black bullhead (N, G) Ictalurus melas Channel Catfish (G) Ictalurus punctatus	—	Black bullhead (N, G) Ictalurus melas Channel Catfish (G) Ictalurus punctatus Stonecat (N) Noturus flavus
Cyprinodontidae	Plains Killifish (G) Fundulus kansae Rio Grande Killifish Fundulus zebrinus Kansae	Plains Killifish (N, G) Fundulus kansae Plains Top Minnow (N, G) Fundulus sciadicus	Plains Killifish (N, G) Fundulus kansae	Rio Grande Killifish (N) Fundulus zebrinus kansae	Plains Killifish (N, G) Fundulus kansae
Poecilidae	Mosquitofish (G) Gambusia affinis	—	Mosquitofish (G) Gambusia affinis	Mosquitofish (N, G) Gambusia affinis	—
Gasterosteidae	—	Brook Stickleback (G) Culaea inconstans	Brook Stickleback (G) Culaea inconstans	—	
Percichthyidae	White Bass (G) Morone chrysops Striped Bass (G) Morone saxatilis	White Bass (G) Morone chrysops	—	—	—
Centrarchidae	Green Sunfish (G) Lepomis cyanellus Bluegill (G) Lepomis macrochirus Smallmouth Bass (G) Micropterus dolomieui Largemouth Bass (G) Micropterus salmoides	Green Sunfish (N, G) Lepomis cyanellus Pumpkinseed (G) Lepomis gibbosus Orangespotted Sunfish (N,G) Lepomis humilis Bluegill (G) Lepomis macrochirus	Black Crappie (G) Pomoxis nigromaculatus Green Sunfish (N, G) Lepomis cyanellus Orangespotted Sunfish (N,G) Lepomis humilis Longear Sunfish Lepomis megalotis	—	Largemouth Bass (G) Micropterus salmoides Green Sunfish (G) Lepomis cyanellus Bluegill (G) Lepomis macrochirus Black Crappie (G) Pomoxis nigromaculatus

FAMILY	COLORADO	PLATTE	ARKANSAS	RIO GRANDE	REPUBLICAN
Centrarchidae (continued)	White Crappie (G) <u>Pomoxis annularis</u> Black Crappie (G) <u>Pomoxis nigromaculatus</u>	Smallmouth Bass (G) <u>Micropterus dolomieui</u> Largemouth Bass (G) <u>Micropterus salmoides</u> White Crappie (G) <u>Pomoxis annularis</u> Black Crappie (G) <u>Pomoxis nigromaculatus</u>			
Percidae	Iowa Darter (G) <u>Etheostoma exile</u> Johnny Darter (N, TC) <u>Etheostoma nigrum</u> Yellow Perch (G) <u>Perca flavescens</u>	Iowa Darter (N, G) <u>Etheostoma exile</u> Johnny Darter (N, TC) <u>Etheastoma nigrum</u> Yellow Perch (G) <u>Perca flavescens</u>	Logperch (G) <u>Percina caprodes</u> Arkansas Darter (N, TC) <u>Etheostoma cragini</u> Walleye (G) <u>Stizostedion vitreum</u>	—	Yellow Perch (G) <u>Perca flavescens</u> Plains Orangethroat Darter (N, TC) <u>Etheostoma spectabile</u> once in Platte
Cottidae	Mottled Sculpin (N, G) <u>Cottus bairdi</u> Piute Sculpin (N, G) <u>Cottus beldingi</u>	—	—	—	—

COMMONLY-ENCOUNTERED GAME FISHES

Family Salmonidae	
Subfamily Salmoninae	
Sockeye (kokanee) salmon	*Oncorhynchus nerka*
Cutthroat trout	*Salmo clarki*
Brown trout	*Salmo trutta*
Rainbow trout	*Salmo gairdneri*
Lake trout	*Salvelinus naymaycush*
Brook trout	*Salvelinus fontinalis*
Family Esocidae	
Northern pike	*Esox lucius*
Family Cyprinidae	
Common (European) carp	*Cyprinus carpio*
Family Ictaluridae	
Channel catfish	*Ictalurus punctatus*
Black bullhead	*Ictalurus melas*
Family Centrarchidae	
Largemouth bass	*Micropterus salmoides*
Smallmouth bass	*Micropterus dolomieui*
Bluegill	*Lepomis macrochirus*
Family Percidae	
Subfamily Percinae	
Yellow perch	*Perca flavescens*
Subfamily Luciopercinae	
Walleye pike	*Stizostedion vitreum*

THREATENED AND ENDANGERED FISHES OF COLORADO

Family Salmonidae

Subfamily salmoninae

Greenback cutthroat trout - *Salmo clarki stomias* (Threatened nationally)
Rio Grande cutthroat trout - *Salmo clarki virginalis* (Threatened Colorado)
Colorado River cutthroat trout - *Salmo clarki pleuriticus* (Threatened Colorado)

Family Cyprinidae

Colorado squawfish - *Ptychocheilus lucius* (Endangered nationally)
Humpback chub - *Gila cypha* (Endangered nationally)
Bonytail chub - *Gila elegans* (Endangered nationally)
Arkansas River speckled chub - *Hybopsis aestivalis tetranemus* (Threatened Colorado)

Family Catostomidae

Razorback sucker - *Xyrauchen texanus* (Endangered Colorado)

Family Percidae

Subfamily Etheostominae

Johnny darter - *Etheostoma nigrum* (Threatened Colorado)
Plains orange throat darter - *Etheostoma spectabile pulchellum* (Threatened Colorado)
Arkansas darter - *Etheostoma cragini* (Threatened Colorado)

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COLLEGE OF AGRICULTURAL AND
ENVIRONMENTAL SCIENCES
DEPARTMENT OF ANIMAL PHYSIOLOGY
AGRICULTURAL EXPERIMENT STATION
ANIMAL PHYSIOLOGY—VERTEBRATE ECOLOGY

DAVIS, CALIFORNIA 95616

AIRMAIL

November 6, 1972

Dr. Robert Behnke
Colorado Cooperative
Fishery Unit
Colorado State University
Fort Collins, Colorado 80521

Dear Dr. Behnke:

Thank you for the reprints and letter of 26 October. We need all the help we can get on our book!

Enclosed is a copy of my checklist of California fishes. I have left off subspecies until I can make up my mind about the validity of many of them.

Sincerely,

Peter Moyle

Peter B. Moyle
Assistant Professor
of Fisheries Biology

PBM:kac
Enclosure

WFB 120 Fall Quarter 1972

NOTES, COMMENTS, AND ADDITIONS TO THE FISH LIST
(September 1972)

Petromyzonidae
Lampetra richardsoni. This is the species the small nonparasitic lamprey of the Sacramento-San Joaquin river resembles the closest. However, Hubbs (1971) indicates they are probably a distinct species, yet undescribed.

Salmonidae
Thymallus arcticus. The arctic grayling has been planted in some lakes in Northern California. Good survival but no evidence of reproduction yet.

Cyprinidae
Plagopterus argentissimus. The woundfin was on the 1959 list of Shapovalov et al., but it does not occur in the state except in a few bait buckets along the Colorado River. It should be removed from the list.
Pogonichthys ciscoides, Clear Lake splittail.
Endemichthys grandipennis, Clear Lake minnow. These two species were recently described by John Hopkirk, 1967 Ph.D. thesis, Berkeley. (In Press, Univ. Calif. Publ. Zool.???)
Gila ~~sp.~~ bicolor snyderi, Owens River tui chub. ~~An undescribed form that probably deserves species status~~ (R. R. Miller).

Ictaluridae
Ictalurus furcatus. The blue catfish was introduced into Southern California in 1969 as is probably now established. (Richardson et al., 1970. Calif. Fish, Game 56(4):311-312.)

Percidae
Stizostedion vitreum. The walleye was introduced into El Capitan Reservoir in Southern California but now apparently has died out.

Centrarchidae
Micropterus coosae, redeye bass.
Micropterus punctulatus, spotted bass. These two species have been introduced into Central Valley streams and reservoirs but their present status is uncertain.

The following marine fishes have been found in mouths of rivers, mostly tributary to Monterey Bay (see Kukowski, 1972. Tech. Pub. 72-2, Moss Landing Marine Lab.)

Atherinidae	
Atherinopsis californiensis.	Jacksmelt
Syngnataidae	
Syngnathus griseolineatus	Bay pipefish
S. californiensis	Kelp pipefish
Embiotocidae	
Amphistichus rhodoterus	Redtail surfperch
A. koelzi	Calico surfperch
Embiotoca jacksoni	Blackperch
Phanerodon furcatus	White seaperch
Scorpaenidae	
Sebastes paucispinis	Bocaccio
Tothidae	
Citharichthys stigmaeus	Speckled sanddab
Pleuroneetidae	
Parophrys vetulus	English sole

FISHES OCCURRING IN THE FRESHWATERS OF CALIFORNIA

An asterisk after a name indicates the species was introduced into California. The numbers in parentheses after the name indicate the following: (1) primary freshwater fishes, those that never enter salt water; (2) secondary freshwater fishes, those that can survive in salt water as well as fresh water but usually spend most of their time in fresh water, also includes anadromous fishes; (3) marine fish which occasionally occur in fresh water.

Petromyzontidae		
Lampetra tridentata	(2)	Pacific lamprey
L. ayresi	(2)	river lamprey
L. richardsoni	(2)	western brook lamprey
L. lethophage	(2)	Pit-Klamath brook lamprey
Acipenseridae		
Acipenser transmontanus	(2)	white sturgeon
Acipenser medirostris	(2)	green sturgeon
Elopidae		
Elops affinis	(3)	machete
Clupeidae		
Clupea harengus	(3)	Pacific herring
Alosa sapidissima*	(2)	American shad
Dorosoma petennse*	(2)	threadfin shad
Osmeridae		
Thaleichthys pacificus	(2)	eulachon
Spirinchus thaleichthys	(3)	Sacramento smelt
Hypomesus pretiosus	(3)	surf smelt
Hypomesus olidus	(3)	pond smelt
Salmonidae		
Prosopium williamsoni	(1)	mountain whitefish
Prosopium gemmiferum*	(1)	Bonneville cisco
Oncorhynchus gorbuscha	(2)	pink salmon
O. Keta	(2)	chum salmon
O. kisutch	(2)	coho salmon
O. tshawytscha	(2)	chinook salmon
O. nerka	(2)	sockeye salmon
O. nerka kennerlyi*	(2)	kokanee
Salmo trutta*	(2)	brown trout
S. clarki	(2)	cutthroat trout
S. gairdneri	(2)	rainbow trout
S. aquabonita	(2)	golden trout
Salvelinus fontinalis*	(2)	brook trout
S. ~~malma~~ Campbelli *	(2)	~~Dolly Varden~~
S. namaycush*	(2)	lake trout

*unpublished name (Cavender)

Cyprinidae		
Cyprinus carpio*	(1)	carp
Carassius auratus*	(1)	goldfish
Tinca tinca*	(1)	tench
Notemigonus crysoleucas*	(1)	golden shiner
Orthodon microlepidotus	(1)	Sacramento blackfish
Mylopharodon conocephalus	(1)	hardhead
Lavinia exilicauda	(1)	hitch
Ptychocheilus grandis	(1)	Sacramento squawfish
Ptychocheilus lucius	(1)	Colorado squawfish
Gila ~~robusta~~ elegans	(1)	bonytail
G. coerulea (= G. bicolor)	(1)	blue chub
G. crassicauda	(1)	thicktail chub
G. bicolor (= Siphateles bicolor)	(1)	Tui chub
G. orcutti	(1)	arroyo chub
G. bicolor mohavensis	(1)	Mojave chub
Pogonichthys macrolepidotus	(1)	splittail
Richardsonius egregius	(1)	Lahontan redside
Hesperoleucus symmetricus	(1)	California roach
Rhinichthys osculus	(1)	speckled dace
Notropis lutrensis*	(1)	red shiner
Pimephales promelas*	(1)	fathead minnow
~~Plagopterus argentissimus~~	~~(1)~~	~~woundfin~~
Cobitidae		
Misgurnus anguillicaudatus*	(1)	weatherfish
Catostomidae		
Ictiobus cyprinellus*	(1)	bigmouth buffalo
Catostomus occidentalis	(1)	Sacramento sucker
C. microps	(1)	Modoc sucker
C. tahoensis	(1)	Tahoe sucker
C. latipinnis	(1)	flannelmouth sucker
C. rimiculus	(1)	Klamath smallscale sucker
C. synderi	(1)	Klamath largescale sucker
C. santaanae	(1)	Santa Ana sucker
C. platyrhynchus	(1)	mountain sucker
C. luxatus	(1)	Lost River sucker
Chamistes brevirostris	(1)	shortnose sucker
Xyrauchen texanus	(1)	humpback sucker
Catostomus fumeiventris Miller		
Ictaluridae		
Ictalurus punctatus*	(1)	channel catfish
I. catus*	(1)	white catfish
I. nebulosus*	(1)	brown bullhead
I. melas*	(1)	black bullhead
I. natalis*	(1)	yellow bullhead
Pylodictis olivaris*	(1)	flathead catfish
I furcatus		blue catfish

Cyprinodontidae		
Fundulus parvipinnis	(2)	California killifish
Cyprinodon macularius	(2)	desert pupfish
C. nevadensis	(2)	Nevada pupfish
C. salinus	(2)	Salt Creek pupfish
C. radiosus	(2)	Owens River pupfish
Lucania parva*	(2)	rainwater killifish
Rivulus harti*	(2)	Hart's rivulus
Cyprinodon milleri LaBounty & Deacon		
Poeciliidae		
Gambusia affinis*	(1)	mosquitofish
Poecilia latipinna*	(1)	sailfin molly
Poecilia mexicana*	(1)	Molly
Xiphophorus variatus*	(1)	varieted platy
Pleuronectidae		
Platichthys stellatus	(3)	starry flounder
Cichlidae		
Tilapia mossambica*	(2)	
Percichthyidae		
Morone saxatilis*	(2)	striped bass
Morone chrysops*	(1)	white bass
Percidae		
Perca flavescens*	(1)	yellow perch
Percina caprodes*	(1)	log perch
Centrarchidae		
Micropterus dolomieui*	(1)	smallmouth bass
M. punctulatus*	(1)	spotted bass
M. salmoides*	(1)	largemouth bass
Lepomis gulosus*	(1)	warmouth
Lepomis cyanellus*	(1)	green sunfish
L. gibbosus*	(1)	pumpkinseed
L. microlophus*	(1)	redear sunfish
L. macrochirus*	(1)	bluegill
Archoplites interruptus	(1)	Sacramento perch
Pomoxis annularis*	(1)	white crappie
P. nigromaculatus*	(1)	black crappie
Mugilidae		
Mugil cephalus	(3)	striped mullet
Embiotocidae		
Cymatogaster aggregata	(3)	shiner perch
Hysterocarpus traski	(2)	tule perch

Cottidae		
Clinocottus acuticeps	(3)	sharpnose sculpin
Cottus gulosus	(2)	riffle sculpin
C. asperrimus	(2)	rough sculpin
C. klamathensis	(2)	marbled sculpin
C. asper	(2)	prickly sculpin
C. beldingi	(2)	Piute sculpin
C. aleuticus	(2)	coastrange sculpin
C. pitensis	(2)	Pit River sculpin
Leptocottus armatus	(3)	Pacific staghorn sculpin
Atherinidae		
Atherinops affinis	(3)	topsmelt
Menidia audens	(2)	Mississippi silversides
Gasterosteidae		
Gasterosteus aculeatus	(2)	threespine stickleback
Elotridae		
Elotris picta	(3)	spotted sleeper
Gobiidae		
Eucyclogobius newberryi	(2)	tidewater goby
Gillichthys mirabilis	(3)	longjaw mudsucker
Clevelandia ios	(3)	arrow goby
Acanthogobius flavimanus	(3)	yellowfin goby

REFERENCES

This checklist is based largely on the 1959 checklist of Shapovalov, Dill, and Cordone. Changes from the 1959 checklist are based on the publications listed below.

1. Bailey, R. M. and C. E. Bond. 1963. Four new species of freshwater sculpins, genus Cottus, from western North America. Occ. Papers Mus. Zool. Univ. Mich. 634:1-27.

2. ____________ et al. 1970. A List of Common and Scientific Names of Fishes from the United States and Canada. Am. Fish Soc. Spec. Pub. No. 6:150.

3. ____________ and T. Uyeno. 1964. Nomenclature of the blue chub and tui chub, cyprinid fishes from western United States. Copeia 1964(1):238-9.

4. Bottroff, L., J. A. St. Amant, and W. Parker. 1969. Addition of Pylodictis olivaris to the California fauna. Cal. Fish and Game 55(1):90.

5. Cook, S. F. and R. L. Moore. 1970. Mississippi silversides, Menidia audens (Atherinidae), established in California. Trans. Am. Fish. Soc. 99U:70-73.

6. Coots, M. 1965. Occurences of the Lost River sucker, Deltistes luxatus (Cope), and shortnose sucker, Chamistes brevirostris (Cope), in Northern California. Calif. Fish and Game 51(2):68-73.

7. Frantz, T. C. and A. J. Cordone. 1965. Introduction of the Bonneville cisco (Prosopium gemmiferum Snyder) into Lake Tahoe. Calif. Fish and Game 51(4):270-5.

8. von Geldern, C. E. 1966. The introduction of white bass (Roccus chrysops) into California. Calif. Fish and Game 52(4):303.

9. Hubbs, C. L. 1971. Lampetra (Entosphenus) lethophaga, new species, the non-parasitic derivative of the Pacific lamprey. Trans. San Diego Nat. Hist. Soc. 16(6):125-164.

10. Hubbs, C. L. and R. R. Miller. 1965. Studies of cyprinodont fishes. XXII Variation in Lucania parva, its establishment in the western United States, and description of a new species from an interior basin in Coahuila, Mexico. Misc. Pub. Mus. Zool., Univ. Mich. 127:104.

11. Johnson, R. L. and L. Shapovalov. 1965. Warmwater gamefishes of California. Calif. Dept. Fish and Game 38 pp.

12. St. Amant, J. A. 1966. Addition of Tilapia mossambica Peters to the California fauna. Calif. Fish and Game 52(1):54-55.

13. ____________ 1970. Addition of Harts Rivulus, Rivulus harti (Boulenger), to the California fauna Calif. Fish and Game 56(2):138.

14. ____________ and F. G. Hoover. 1969. Addition of Misgurnus anguilicaudatus (Cantor) to the California fauna. Calif. Fish and Game 55(4):330-1.

15. ____________ and Ira Sharp. 1971. Addition of Xiphophorus variatus (meak) to the California fauna. Calif. Fish and Game 57(2):128-9.

16. Schreck, C. B. and R. J. Behnke. Trouts of the upper Kern River Basin, California, with reference to systematics and evolution of western North American _Salmo_ J. Fish Res. Bd. Canada 28:987-998.

17. Shapovalov, L., W. A. Dill, and A. J. Cordone. 1959. A revised checklist of the freshwater and anadromous fishes of California. Calif. Fish and Game 45(3):159-180.

18. Smith, G. R. 1966. Distribution and evolution of the North American catostomid fishes of the subgenus _Pantosteus_, genus _Catostomus_. Misc. Pub. Mus. Zoology, Univ. Mich. 129:133.

Peter B. Moyle
26 June 1972

The Distributional History

of the

Biota of the Southern Appalachians

PART III: VERTEBRATES

A Symposium Sponsored by
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the Association of Southeastern Biologists,
Held at Blacksburg, Virginia
June 25 - 27, 1970

Edited by Perry C. Holt
with the Assistance of
Robert A. Paterson and John P. Hubbard

Research Division Monograph 4
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Fishes of the Central Appalachian Drainages: Their Distribution and Dispersal

Robert E. Jenkins, Ernest A. Lachner, Frank J. Schwartz

The great diversity of the fish fauna of the central Appalachian drainages and the presence of numerous endemic species were recognized by Cope (1868, 1869, 1870), Jordan (1889, 1928) and Jordan with collaborators (as Jordan and Brayton, 1878). Through the efforts of many individuals, particularly during the past three decades, a large amount of information has accumulated on this ichthyofauna. Although undescribed forms continue to be discovered, patterns of distribution and diversity by drainage systems and intra-drainage distribution and phylogenetic relationships of most species have been sufficiently studied to permit zoögeographic analysis.

The 313 native freshwater species and subspecies treated herein primarily constitute stream faunas. The study region was not glaciated, and partly for this reason it has very few natural lakes. These include the Carolina Bays and other lakes and ponds in swampy sections of the outer Coastal Plain (Berg, 1963; Gerking, 1963; Yount, 1963). Mountain Lake in Virginia (Roth and Neff, 1964) is the only natural montane lake in the region; it is spring-fed and has a depauperate fauna. Many large, river channels were impounded during the past four decades and other reservoirs have been proposed.

Most of the drainages originating in the central Appalachian Mountains are treated (fig. 1). Coverage includes those drainages in montane, Piedmont and plateau provinces, other uplands, and the Atlantic Coastal Plain and Ohio Valley lowlands. The drainages are separated into two groups by the Atlantic slope-Ohio basin divide. The group of Atlantic slope drainages treated extends from the Peedee northward to the Potomac. The Peedee was selected as the southerly Atlantic slope drainage for treatment in our study in order to complement that by Ramsey (1965; this symposium, hereinafter referred to as Ramsey, ms.) which terminated in the Santee drainage, the first drainage south of the Peedee. Systems omitted that lie entirely on the Coastal Plain are the Lake Waccamaw system of South and North Carolina (Hubbs and Raney, 1946), the Carolina Bay Lakes (Frey, 1951; Collette, 1962), the Dismal Swamp-Nansemond system of North Carolina and Virginia (under study by R. D. Ross) and other small systems. Drainages treated west of the divide, from the Monongahela to the Tennessee, are contained within the upper and southern parts of the Ohio River basin, a major segment of the vast Mississippi River basin. Drainages within the State of Kentucky between the Big Sandy and Cumberland drainages are not treated, although their endemic fishes are noted. The area we treat includes a major portion of the North American freshwater fish fauna.

Our concept of the diversity of the central Appalachian fish fauna compared with those of other regions stems from our field work in eastern United States, current work of other individuals and the literature. Studies of particular interest are: southeastern United States (Ramsey, 1965; Gibbs, 1957a; Randall, 1958; Bailey, Winn and Smith, 1954; Smith-Vaniz, 1968); Texas (Clark Hubbs, 1957); northern Ohio basin (Raney, 1939; Trautman, 1957; Gerking, 1945); upper Mississippi basin (Forbes and Richardson, 1920; Cleary, 1956; Greene, 1935; Underhill, 1957; Eddy, Moyle and Underhill, 1963); Missouri (Pflieger, 1969); Missouri basin (Metcalf, 1966; Bailey and Allum, 1962; Willock, 1969); New England, Great Lakes region and associated drainages (Whitworth, Berrien and Keller, 1968; McCab, 1943; Hubbs and Lagler, 1958; Radforth, 1944; Livingstone, 1953; Lindsey, 1956); and western United States (Hubbs and Miller, 1948; Miller, 1959, 1965).

This study of the fish fauna of the central Appalachian drainages summarizes the geographical and the ecological distribtuions of the many species and most subspecies, and identifies patterns of distribtuion and diversity, centers of evolution and dispersal, possible means of isolation and routes of dispersal. Our approach is largely one of distinguishing and relating faunas, by drainage systems, with particular reference to drainage history and physical barriers. While it appears that ecoolgical distributional problems will be emphasized more in future zoögeographic studies, it will remain necessary in many of those studies to consider historical factors such as species and drainage evolution as well.

SCOPE AND METHODS

The following words used in this treatment are defined: *System,* a group of interconnected streams within a drainage; *Drainage,* an interconnected major group of streams, or systems entering the marine habitat, or the Ohio River (such as the Roanoke and Cumberland drainages); *Basin,* a group of interconnected drainages (such as the Ohio, Mississippi and Missouri). The terms *Atlantic slope* and *Gulf* (*of Mexico*) *slope* are used to refer collectively to all drainages on their surfaces, except for the Mississippi River drainage proper on the Gulf slope.

DRAINAGES.—Drainages treated from the Peedee northward to the Roanoke provide excellent coverage of the montane, upland and lowland faunas of the south-central Atlantic slope, even though minor (small-sized Coastal Plain) drainages were not given detailed treatment (fig. 1). Drainages from the James to the Potomac include nearly all freshwater species of the western Chesapeake Bay basin. The Susquehanna, the only major Chesapeake drainage north of the Potomac, is regarded as out of the limits of the central Appalachians. Collections from it have been taken by us, and its fauna in

New York was documented by Greeley (1936). The Tennessee and Cumberland drainages have fish faunas that are among the richest in North America. Remaining drainages of the Ohio basin, except for the Monongahela, enter the Ohio River from the south and are referred to as the south-central Ohio basin. The Monongahela is a major drainage of the upper Ohio basin; it joins the Allegheny River to form the Ohio. Studies treating the northern and upper Ohio basin and Ohio River are noted above.

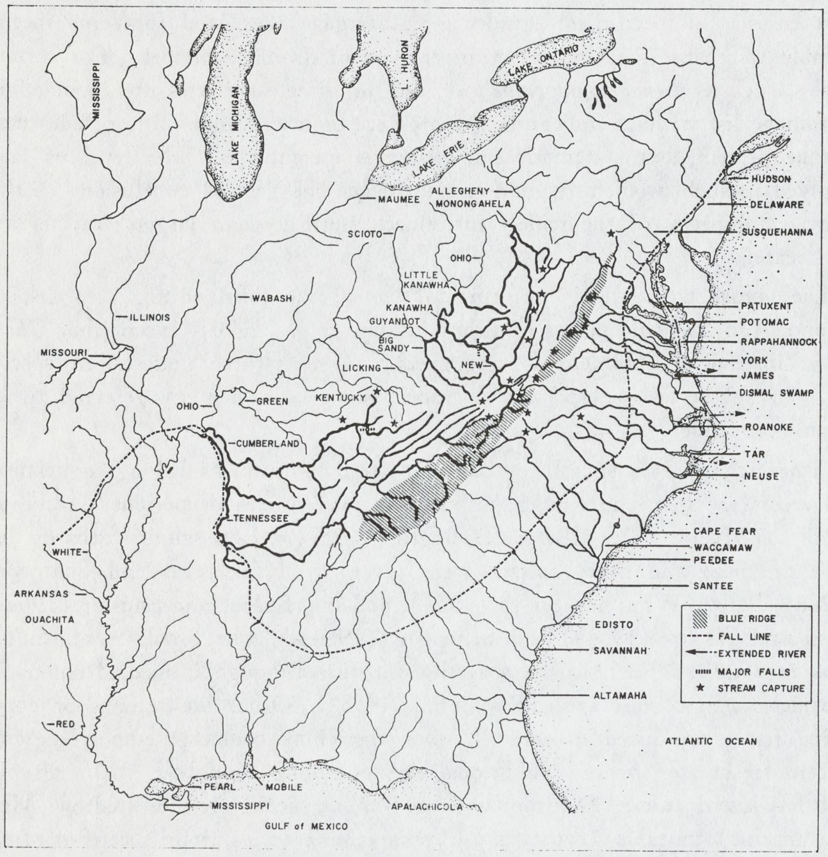

FIGURE 1—Major drainages of eastern United States. The drainages treated in the Ohio basin are shown by heaviest lines. Atlantic slope drainages studied are shown by lines of moderate thickness. Theaters of stream capture are indicated by stars. Ross (ms.) discusses additional captures involving the Tennessee drainage. (Only the lower portions of major drainages tributary to the west side of the Mississippi River are shown).

FISHES.—Although our main intent is to treat the Appalachian fish fauna, lowland fishes were included for several reasons: (1) to contrast patterns of distribution, diversity and evolution of Appalachian and lowland fishes; (2) because it is often difficult, and in many cases impossible, to segregate drainage faunas into Appalachian and lowland faunas, due to inhabitation of a wide range of environmental conditions by numerous species, enhanced by transition or interdigitation of habitat types; (3) because pertinent details of the ecology and range limits of many species are poorly known.

Subspecies that have been adequately studied and defined are included in most cases. Subspecific intergrades in a drainage are listed for some species in table 1, because they indicate transgression of drainage divides. For certain species, such as *Etheostoma flabellare,* one to three subspecies are included in a drainage list without indicating the presence of intergrades. Intergrades may also be present, but systematic knowledge is incomplete. The level of taxa involved in such problems should not influence the general conclusions of this study. Subspecies of the widely introduced sunfishes and larger catfishes are not treated.

The nomenclature used conforms to that of the third edition of a list of common and scientific names of fishes (Bailey *et al.,* 1970), except that *Chrosomus* instead of *Phoxinus* is recognized. Twenty-three undescribed species (sp.) or subspecies (subsp.) are included, some of which are referred to by a common name.

Fishes regarded as strictly or basically freshwater forms belong to primary and secondary division families, or are vicarious species of peripheral division families (Myers, 1938, 1949; Darlington, 1957). Low-salinity records for some of these and other species were given by Hildebrand and Schroeder (1928), Bailey, Winn and Smith (1954), deSylva, Kalber and Shuster (1962), Keup and Bayles (1964), and Schwartz (1964). The brook trout, *Salvelinus fontinalis,* is included as a freshwater fish although it is diadromous in latitudes north of our area (Rounsefell, 1958). Other diadromous or euryhaline fishes are listed in table 1 since they may compete temporally with strictly freshwater fishes. Additional species might have been included, but with less justification. Diadromous or euryhaline species are indicated by "Ma" (for marine) in table 1; they are *Petromyzon marinus,* four species of *Lepisosteus,* one species of *Anguilla,* three clupeids, *Fundulus diaphanus, Gambusia affinis,* and two percichthyids, *Morone americanus* and *M. saxatilis* (Gunter, 1956; Suttkus, 1963:66). *Lepisosteus oculatus* and *L. platostomus* were arbitrarily included as euryhaline species, although they, along with *Alosa chrysochloris* and *Dorosoma petenense,* are known only from freshwater in the area.

Table 1.—*The fishes of the central Appalachian drainages and their general habitat.*

DRAINAGE OCCURRENCE, E = endemic, N = native, NP = probably present — native, NI = regarded as native but possibly introduced, I = introduced, IP = probably or possibly introduced — regarded as such, Ma = euryhaline or diadromous.

NATIVE EXTRALIMITAL DISTRIBUTION, So = south on Atlantic slope, No = north on Atlantic slope, O = predominantly Ohio basin form, M = lower and/or central Mississippi basin, G = Gulf of Mexico slope. X = category most frequently inhabited.

	Habitat						Drainage Occurrence																		Native Extralimital Distribution	
							Atlantic Slope									Ohio Basin										
	Lowland	Upland	Montane	Big River	Stream	Creek	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee	Atlantic slope	Elsewhere
PETROMYZONTIDAE																										
Ichthyomyzon bdellium	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	N	N	—	—	—	N	—	N	—	O
I. castaneus	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
I. greeleyi	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	O
I. hubbsi	—	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
Lampetra aepyptera	—	x	—	—	x	x	—	—	N	NP	NP	N	N	N	N	N	N	N	—	—	N	NP	—	N	No	GM
L. lamottei	—	x	—	—	x	x	—	—	—	—	N	NP	NP	N	N	—	N	—	—	—	N	NP	—	N	No	M
Petromyzon marinus	—	—	—	—	—	—	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	—	—	—	—	—	—	—	—	NoSo	—
ACIPENSERIDAE																										
Acipenser fulvescens	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
Scaphirhynchus platorynchus	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
POLYODONTIDAE																										
Polyodon spathula	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	N	N	—	—	—	N	—	N	—	GM
LEPISOSTEIDAE																										
Lepisosteus oculatus	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Ma	—	Ma	—	GM
L. osseus	x	x	—	x	x	—	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	—	Ma	Ma	—	Ma	NoSo	GM
L. platostomus	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Ma	—	Ma	—	GM
L. spatula	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Ma	—	GM
AMIIDAE																										
Amia calva	x	—	—	x	x	—	N	N	N	N	N	N	N	—	N	—	—	—	I	—	—	—	—	N	NoSo	GM
ANGUILLIDAE																										
Anguilla rostrata	—	—	—	—	—	—	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	—	Ma	Ma	—	Ma	NoSo	GM
CLUPEIDAE																										
Alosa chrysochloris	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	Ma	—	—	Ma	Ma	—	Ma	—	GM
Dorosoma cepedianum	x	x	—	x	x	—	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	Ma	—	—	Ma	Ma	—	Ma	NoSo	GM
D. petenense	x	—	—	x	—	—	I	—	—	—	I	—	—	—	—	—	—	I	I	—	—	Ma	—	Ma	—	GM

	HABITAT						DRAINAGE OCCURRENCE: Atlantic Slope									DRAINAGE OCCURRENCE: Ohio Basin									NATIVE EXTRALIMITAL DISTRIBUTION	
	Lowland	Upland	Montane	Big River	Stream	Creek	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee	Atlantic slope	Elsewhere
HIODONTIDAE																										
Hiodon alosoides	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	N	N	—	N	—	M
H. tergisus	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	N	—	N	—	M
SALMONIDAE																										
Oncorhynchus nerka	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	—	—	—	—	—	—	—	—	—	—
Salmo gairdneri	—	—	—	—	—	—	I	—	—	—	I	I	—	I	I	I	—	I	I	—	—	I	I	I	—	—
S. trutta	—	—	—	—	—	—	I	—	—	—	I	I	—	I	I	I	—	I	I	—	—	I	—	I	—	—
Salvelinus fontinalis	—	—	x	—	x	x	IP	—	—	—	N	N	—	NI	N	N	I	IP	N	—	—	IP	IP	N	NoSo	—
UMBRIDAE																										
Umbra pygmaea	x	—	—	—	x	x	N	N	N	N	N	N	N	—	N	—	—	—	—	—	—	—	—	—	NoSo	—
ESOCIDAE																										
Esox a. americanus	x	—	—	—	x	x	N	N	N	N	N	N	N	N	N	I	—	—	—	—	—	—	—	—	NoSo	G
E. a. vermiculatus	x	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
E. lucius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	I	—	—	—	—	—	—	—	—	—	M
E. masquinongy ohiensis	x	x	—	x	x	—	—	—	—	—	I	I	—	—	I	N	N	N	IP	—	—	N	—	N	—	O
E. niger	x	x	—	—	x	x	N	N	N	N	N	N	N	N	N	I	—	I	I	—	—	—	—	N	NoSo	GM
CYPRINIDAE																										
Campostoma a. anomalum	—	x	x	—	x	x	—	—	—	—	—	—	—	—	N	N	N	N	—	N	N	N	N	N	No	O
C. a. michauxi	—	x	x	—	x	x	IP	—	—	—	N	N	—	—	—	—	—	—	N	—	—	—	—	N	So	—
Carassius auratus	—	—	—	—	—	—	I	—	—	—	I	—	—	—	I	—	—	I	—	—	—	I	I	I	—	—
Chrosomus erythrogaster	—	x	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	N	—	—	N	N	N	N	—	M
C. o. oreas	—	x	x	—	—	x	—	—	N	N	N	N	N	IP	IP	—	—	—	N	—	—	—	—	IP	—	—
C. oreas subsp.	—	x	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
Clinostomus elongatus	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	No	M
C. f. funduloides	—	x	—	—	—	x	N	N	N	N	N	N	N	N	N	N	—	—	N	—	N	—	—	—	NoSo	O
C f. estor	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
C. funduloides subsp.	—	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—
Cyprinus carpio	—	—	—	—	—	—	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	—	—
Ericymba buccata	—	x	—	—	x	x	—	—	—	—	—	—	—	N	N	N	N	N	N	N	N	N	N	N	No	GM
Exoglossum laurae	—	x	x	—	x	—	—	—	—	—	—	—	—	—	—	NI	—	—	N	—	—	—	—	—	—	O
E. maxillingua	—	x	—	—	x	—	—	—	—	—	N	N	N	N	N	—	—	—	NI	—	—	—	—	—	No	—
Hemitremia flammea	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	G
Hybognathus n. nuchalis	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
H. n. regius	x	x	—	x	x	—	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	NoSo	—
Hybopsis aestivalis hyostoma	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	N	N	—	N	—	GM
H. a. amblops	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	N	N	N	—	—	N	N	—	N	—	M
H. cahni	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—

H. d. dissimilis	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	N	N	N	N	—	N	N	—	N	—	O
H. hypsinotus	—	x	—	—	x	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
H. i. insignis	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
H. i. eristigma	—	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
H. labrosa	—	x	—	—	x	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
H. monacha	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
H. storeriana	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	N	N	N	—	—	N	N	—	N	—	GM
Leuciscus idus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	—	—	—	—	—	—	—	—	—	—	—
Nocomis effusus	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	O
N. l. leptocephalus	—	x	x	—	x	x	N	N	N	N	N	N	N	IP	IP	—	—	—	N	—	—	—	—	—	So	—
N. l. bellicus	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	G
N. l. interocularis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	IP	—	—
N. micropogon	—	x	x	x	x	—	—	—	—	—	—	N	N	N	N	N	N	N	—	N	N	N	N	N	No	O
N. platyrhynchus	—	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—
N. raneyi	—	x	—	x	x	—	—	—	N	N	N	NI	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Notemigonus crysoleucas	x	x	—	—	x	x	N	N	N	N	N	N	N	N	N	N	—	N	—	—	—	N	—	N	NoSo	GM
Notropis albeolus	—	x	—	—	x	x	—	N	N	N	N	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—
N. alborus	—	x	—	—	x	x	N	N	N	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. altipinnis	x	x	—	—	—	x	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
N. amnis	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	GM
N. amoenus	x	x	—	x	x	—	—	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
N. a. analostanus	—	x	—	—	x	—	—	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
N. a.: a. X chloristius	—	x	—	—	x	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. ardens	—	x	—	—	x	x	—	—	N	N	N	N	—	—	IP	—	—	—	N	—	—	N	N	N	—	O
N. ariommus	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—	N	N	—	N	—	O
N. atherinoides	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—	N	N	N	N	No	GM
N. baileyi	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	G
N. bellus	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	G
N. bifrenatus	x	x	—	—	—	x	—	—	N	NP	N	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
N. blennius	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	N	N	N	—	N	—	M
N. boops	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	M
N. buchanani	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	N	—	N	—	GM
N. cerasinus	—	x	—	—	x	x	—	IP	—	—	N	NI	—	—	—	—	—	—	N	—	—	—	—	—	—	—
N. chalybaeus	x	—	—	—	—	x	N	N	N	N	N	—	—	—	N	—	—	—	—	—	—	—	—	—	NoSo	GM
N. chiliticus	—	x	—	—	x	x	N	—	—	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. c. chrysocephalus	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	N	N	N	—	N	N	N	N	N	—	M
N. coccogenis	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	IP	—	—	—	—	N	So	—
N. cornutus	—	x	x	—	x	x	—	—	—	—	—	N	N	N	N	—	—	N	—	—	—	—	—	—	No	M
N. c. cummingsae	x	—	—	—	x	—	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	G
N. d. dorsalis	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	M
N. emiliae	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	So	GM
N. fumeus	x	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	GM
N. galacturus	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	NI	—	—	N	—	N	—	M
N. heterolepis	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	No	M
N. hudsonius	x	x	—	x	x	—	N	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	NoSo	M
N. leuciodus	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	IP	—	—	N	—	N	So	O
N. lirus	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	G
N. lutipinnis	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	IP	So	—
N. maculatus	x	—	—	—	x	x	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	GM
N. niveus	—	x	—	—	x	—	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
N. petersoni	x	—	—	—	x	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	G
N. photogenis	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	N	N	N	N	—	N	—	O
N. p. procne	x	x	—	—	x	x	—	—	—	—	—	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
N. p. longiceps	x	x	—	—	x	x	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
N. pyrrhomelas	—	x	—	—	x	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—

	Habitat						Drainage Occurrence: Atlantic Slope									Drainage Occurrence: Ohio Basin									Native Extralimital Distribution	
	Lowland	Upland	Montane	Big River	Stream	Creek	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee	Atlantic slope	Elsewhere
N. r. rubellus	—	x	x	—	x	x	—	—			—	N	N	N	N	N	N	N	N	N	N	—	N?	—	No	M
N. r. micropteryx	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
N. rubricroceus	—	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	IP	—	—	—	—	N	So	—
N. scabriceps	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—
N. scepticus	—	x	—	—	x	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
N. semperasper	—	x	—	—	x	—	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. shumardi	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	GM
N. s. spectrunculus	—	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
N. spectrunculus subsp.	—	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
N. s. spilopterus	—	x	—	x	x	—	—	—	—	—	—	—	—	—	N	N	N	N	N	N	N	N	N	N	No	M
N. stilbius	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	GM
N. s. stramineus	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	N	N	N	N	N	N	N	—	N	—	M
N. telescopus	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	IP	—	—	N	—	N	—	M
N. umbratilus cyanocephalus	x	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	N	—	N	—	M
N. v. volucellus	—	x	—	x	x	—	—	—	N	N	N	NI	—	—	—	N	N	N	N	N	N	N	N	N	—	GM
N. v. wickliffi	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	N	—	—	—	—
N. whipplei	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	N	N	N	N	—	M
N. sp. (paleband shiner)	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
N. sp. (sawfin shiner)	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
N. sp. (*longirostris* group)	x	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	M
N. sp. (*stramineus* group)	—	x	—	—	x	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phenacobius crassilabrum	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
P. mirabilis	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	N	N	—	N	—	GM
P. teretulus	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—
P. uranops	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	O
Pimephales notatus	—	x	—	x	x	—	—	—	—	—	IP	IP	—	—	N	N	N	N	N	N	N	N	N	N	No	GM
P. promelas	—	x	—	—	x	x	—	—	—	—	—	—	—	—	I	I	I	IP	—	—	—	N	IP	N	No	GM
P. vigilax perspicuous	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—	N	N	IP	N	—	GM
Rhinichthys a. atratulus	—	x	x	—	x	x	N	—	—	—	N	N	N	N	N	—	—	—	IP	—	—	—	—	—	No	—
R. a. meleagris	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	N	—	—	—	N	N	—	—	—	—	M
R. a. obtusus	—	x	x	—	x	x	—	—	—	—	—	—	—	—	N	N	—	N	N	—	N	N	N	N	So	O
R. cataractae	—	x	x	—	x	x	—	—	—	—	—	N	N	N	N	N	—	N	N	—	N	—	—	N	NoSo	O
Semotilus atromaculatus	—	x	x	—	x	x	N	N	N	N	N	N	N	—	N	N	N	N	N	N	N	N	N	N	NoSo	GM
S. corporalis	—	x	—	x	x	—	—	—	—	—	—	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
S. m. margarita	—	x	x	—	—	x	—	—	—	—	—	—	—	—	N	N	—	—	—	—	—	—	—	—	No	—
S. sp.	x	—	—	—	—	x	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tinca tinca	—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	—	—	—	—	—	—	—	—	—	—	—

CATOSTOMIDAE																										
Carpiodes c. carpio	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	N	—	N	—	GM
C. cyprinus	x	x	—	x	—	—	NI	—	—	—	N	N	—	—	N	N	N	N	—	N	N	N	—	N	NoSo	GM
C. velifer	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—	N	N	—	N	—	GM
Catostomus catostomus	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	—	—
C. c. commersonii	—	x	x	—	x	x	N	NI	NI	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	NoSo	M
Cycleptus elongatus	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
Erimyzon o. oblongus	x	x	—	—	x	x	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	NoSo	—
E. o. claviformis	x	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
E. sucetta	x	—	—	—	x	—	N	N	N	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	NoSo	GM
Hypentelium nigricans	—	x	x	—	x	x	N	—	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	NoSo	GM
H. roanokense	—	x	—	—	x	x	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ictiobus bubalus	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	N	N	—	N	—	GM
I. cyprinellus	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	N	—	N	—	GM
I. niger	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	N	—	N	—	GM
Lagochila lacera	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	M
Minytrema melanops	x	x	—	x	x	—	N	N	—	—	—	—	—	—	—	N	N	N	—	N	N	N	—	N	So	GM
Moxostoma anisurum	x	x	—	x	x	—	N	N	N	N	N	—	—	—	—	N	—	N	—	—	N	N	N	N	So	M
M. ariommum	—	x	—	—	x	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
M. carinatum	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	—	N	N	N	—	N	—	GM
M. cervinum	—	x	—	—	x	x	—	—	N	N	N	NI	—	—	—	—	—	—	—	—	—	—	—	—	—	—
M. duquesnii	—	x	x	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	—	N	N	N	N	N	—	GM
M. erythrurum	—	x	—	x	x	—	—	—	—	—	N	N	—	—	—	N	N	N	—	N	N	N	N	N	—	GM
M. hamiltoni	—	x	—	—	x	x	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
M. m. macrolepidotum	x	x	—	x	x	—	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	NoSo	M
M. m. breviceps	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	—	—	N	N	—	N	—	O
M. pappillosum	x	x	—	x	x	—	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
M. rhothoecum	—	x	x	—	x	x	—	—	—	—	N	N	—	—	N	—	—	—	N	—	—	—	—	—	—	—
M. robustum	—	x	—	—	x	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
ICTALURIDAE																										
Ictalurus brunneus	x	x	—	x	x	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	G
I. catus	x	x	—	x	—	—	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	NoSo	G
I. furcatus	x	—	—	x	—	—	—	—	—	—	—	—	—	—	I	N	—	N	IP	—	—	N	—	N	—	GM
I. melas	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	—	IP	—	N	N	IP	N	—	GM
I. natalis	x	x	—	—	x	—	N	N	N	N	N	N	N	N	N	N	N	N	—	—	N	N	N	N	NoSo	GM
I. nebulosus	x	x	—	x	x	—	N	N	N	N	N	N	N	N	N	N	—	N	—	—	—	N	IP	N	NoSo	GM
I. platycephalus	x	x	—	x	x	—	N	N	NI	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
I. punctatus	x	x	—	x	x	—	IP	IP	IP	IP	IP	IP	IP	IP	IP	N	N	N	NI	N	N	N	NI	N	So	GM
Noturus baileyi	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
N. elegans	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	O
N. eleutherus	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	N	—	N	—	M
N. exilis	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	M
N. flavipinnis	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
N. flavus	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	N	N	—	—	—	N	N	—	N	—	M
N. furiosus	x	x	—	—	x	—	—	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. gilberti	—	x	—	—	x	—	—	—	—	—	N	NI	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. gyrinus	x	—	—	—	x	x	N	N	N	N	N	N	N	—	N	—	—	—	—	—	—	N	—	N	NoSo	GM
N. insignis	—	x	—	—	x	x	N	N	N	N	N	N	N	N	N	IP	—	—	N	—	—	—	—	IP	NoSo	—
N. miurus	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	N	N	N	—	N	—	N	—	N	—	GM
N. nocturnus	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	N	—	N	—	GM
Pylodictis olivaris	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	N	—	N	N	N	N	—	GM
AMBLYOPSIDAE																										
Chologaster agassizi	x	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	M
C. cornuta	x	—	—	—	x	x	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
Typhlichthys subterraneus	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM

	Habitat						Drainage Occurrence: Atlantic Slope									Drainage Occurrence: Ohio Basin									Native Extralimital Distribution	
	Lowland	Upland	Montane	Big River	Stream	Creek	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee	Atlantic slope	Elsewhere
APHREDODERIDAE																										
Aphredoderus sayanus	x	—	—	—	x	x	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	N	—	N	NoSo	GM
PERCOPSIDAE																										
Percopsis omiscomaycus	—	x	—	—	x	—	—	—	—	—	—	—	—	—	N	N	N	N	—	N	—	—	—	—	No	M
CYPRINODONTIDAE																										
Fundulus albolineatus	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
F. catenatus	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	N?	N	—	M
F. d. diaphanus	x	x	—	—	x	—	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	—	—	—	—	—	—	—	—	No	—
F. notatus	x	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
F. lineolatus	x	—	—	—	x	x	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	So	G
F. olivaceus	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
F. rathbuni	—	x	—	—	x	—	N	N	N	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F. stellifer	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	IP	—	G
Fundulus sp.	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
POECILIIDAE																										
Gambusia a. affinis	x	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Ma	IP	Ma	—	GM
G. a. holbrooki	x	x	—	—	x	x	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	—	—	—	—	—	—	—	—	NoSo	G
Heterandria formosa	x	—	—	—	—	x	NP	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	G
ATHERINIDAE																										
Labidesthes sicculus	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	N	—	N	—	N	N	N	N	N	So	GM
GASTEROSTEIDAE																										
Culaea inconstans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	—	—
COTTIDAE																										
Cottus baileyi	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
C. b. bairdii	—	x	x	—	x	x	—	—	—	—	N	N	—	N	N	N	N	N	N	N	—	—	—	—	No	M
C. bairdii subsp.	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	N	—	—
C. c. carolinae	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	M
C. carolinae subsp.	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	E?	—	—	—	—	—	—	—
C. cognatus	—	x	—	—	x	x	—	—	—	—	—	N	—	—	N	—	—	—	—	—	—	—	—	—	No	—
C. sp. (smoky sculpin)	—	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	So	—
PERCICHTHYIDAE																										
Morone americanus	x	—	—	x	x	—	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	—	—	—	—	—	—	—	—	NoSo	—
M. chrysops	x	x	—	x	x	—	I	—	—	—	I	—	—	—	—	I	NI	—	IP	—	—	N	—	N	—	GM
M. mississippiensis	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	IP	N	—	N	—	GM
M. saxatilis	x	—	—	x	x	—	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	Ma	—	—	—	—	—	—	Ma	—	Ma	NoSo	G

CENTRARCHIDAE																										
Acantharcus pomotis	x	—	—	—	x	x	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	NoSo	—
Ambloplites cavifrons	—	x	—	—	x	—	—	—	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. r. rupestris	—	x	x	x	x	—	IP	—	I	—	I	IP	—	I	I	N	N	N	N	N	N	N	N	N	—	M
Centrarchus macropterus	x	—	—	—	x	—	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	So	M
Elassoma evergladei	x	—	—	—	x	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
E. zonatum	x	—	—	—	x	—	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	N	So	GM
E. sp.	x	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	M
Enneacanthus chaetodon	x	—	—	—	x	—	N	N	N	NP	NP	—	—	—	—	—	—	—	—	—	—	—	—	—	NoSo	—
E. gloriosus	x	—	—	—	x	—	N	N	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	NoSo	G
E. obesus	x	—	—	—	x	—	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	NoSo	—
Lepomis auritus	—	x	—	—	x	x	N	N	N	N	N	N	N	N	N	—	—	—	IP	—	—	—	—	IP	NoSo	G
L. cyanellus	—	x	—	—	x	—	I	I	I	I	I	—	—	—	I	N	N	N	IP	N	N	N	NI	N	—	GM
L. gibbosus	—	x	—	—	x	x	N	N	N	N	N	N	N	N	N	—	—	N	IP	—	—	IP	—	IP	NoSo	M
L. gulosus	—	x	—	x	x	—	N	N	N	N	N	N	N	—	IP	—	—	N	IP	—	—	N	IP	N	So	GM
L. humilis	x	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	IP	—	—	—	—	N	—	N	—	GM
L. macrochirus	x	x	—	x	x	—	NI	NI	IP	IP	IP	IP	IP	IP	IP	N	N	N	IP	N	N	N	NI	N	So	GM
L. marginatus	x	—	—	—	x	—	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	N	So	GM
L. megalotis	—	x	—	—	x	x	—	—	—	—	—	—	—	—	I	N	N	N	I	N	N	N	N	N	—	GM
L. microlophus	x	x	—	—	x	—	NI	NI	IP	IP	—	—	—	—	I	IP	—	—	—	—	—	N	—	N	So	GM
L. punctatus	x	—	—	—	x	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	So	GM
Micropterus coosae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	—	—	G
M. d. dolomieui	—	x	—	—	x	x	I	—	I	—	I	I	I	I	I	N	N	N	N	N	N	N	N	N	—	M
M. p. punctulatus	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	NI	N	N	N	N	N	—	M
M. s. salmoides	x	x	—	x	x	—	N	N	N	N	N	IP	IP	IP	IP	N	N	N	IP	—	N	N	IP	N	So	GM
Pomoxis annularis	x	x	—	x	x	—	I	I	I	—	I	I	—	I	I	N	N	N	IP	—	N	N	IP	N	—	GM
P. nigromaculatus	x	x	—	x	x	—	N	N	N	N	N	IP	IP	IP	IP	N	—	N	IP	—	—	N	—	N	So	GM
PERCIDAE																										
Ammocrypta asprella	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	GM
A. clara	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	M
A. pellucida	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	N	N	N	—	—	N	N	—	N	—	GM
Etheostoma acuticeps	—	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. atripinne	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—
E. b. blennioides	—	x	x	—	x	x	—	—	—	—	—	—	—	—	N	N	N	N	N	N	N	—	—	—	—	O
E. b. gutselli	—	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. b.: n. X *gutselli*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. b. newmanii	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	N	N	—	M
E. blennius	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. caeruleum	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	N	N	N	—	N	N	N	N	N	—	M
E. camurum	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	—	—	—	N	—	N	—	O
E. chlorosomum	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	GM
E. cinereum	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
E. c. collis	x	x	—	—	—	x	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
E. c. lepidinion	x	x	—	—	—	x	—	N	N	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E. duryi	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. f. flabellare	—	x	x	—	x	x	—	N	N	N	N	N	—	N	N	N	N	N	N	—	N	N	—	N	No	M
E. f. brevispinna	—	x	x	—	x	x	N	—	—	—	N	—	—	—	—	—	—	—	N	—	—	—	—	N	So	—
E. f. lineolatum	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	N	—	M
E. fusiforme fusiforme	x	—	—	—	—	x	—	N	N	N	N	N	—	—	N	—	—	—	—	—	—	—	—	—	No	—
E. f. barratti	x	—	—	—	—	x	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	IP	So	GM
E. gracile	x	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
E. histrio	x	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	GM
E. kanawhae	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—	—	—	—
E. kennicotti	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	N	—	O
E. longimanum	—	x	—	—	x	x	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E. luteovinctum	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—

	Habitat						Drainage Occurrence: Atlantic Slope									Drainage Occurrence: Ohio Basin									Native Extralimital Distribution	
	Lowland	Upland	Montane	Big River	Stream	Creek	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee	Atlantic slope	Elsewhere
E. m. maculatum	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	O
E. m. sanguifluum	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—
E. m. vulneratum	—	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. mariae	x	x	—	—	x	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E. microlepidum	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—
E. n. nigrum	—	x	—	—	x	x	—	—	N	N	N	N	N	—	—	N	N	N	N	N	N	N	N	N	No	GM
E. obeyense	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—
E. o. olmstedi	x	x	—	—	x	x	—	—	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	No	—
E. o.: o. X atromaculatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	—	—	—
E. o. atromaculatum	x	x	—	—	x	x	—	—	—	—	N	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
E. o.: o. X vexillare	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	—	—	—	—	—
E. o. vexillare	—	x	—	—	x	x	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	—	—	—	—
E. o. maculaticeps	x	x	—	—	x	x	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
E. osburni	—	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	N	E	—	—	—	—	—	—	—
E. podostemone	—	x	—	—	x	x	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E. proeliare	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	GM
E. rufilineatum	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
E. s. sagitta	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	E	—	—	—
E. serriferum	x	—	—	—	x	—	N	N	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
E. simoterum	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. s. spectabile	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	M
E. squamiceps	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	O
E. s. stigmaeum	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	GM
E. s. jessiae	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
E. swannanoa	—	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. tippecanoe	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	N	N	—	—	—	N	—	N	—	O
E. tuscumbia	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. variatum	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	N	N	N	—	—	N	—	—	—	—	O
E. virgatum	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—
E. vitreum	—	x	—	—	x	—	—	—	N	N	N	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
E. z. zonale	—	x	x	—	x	x	—	—	—	—	—	—	—	—	—	N	N	N	—	N	N	N	—	N	—	M
E. sp. (dusttail darter)	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. sp. (Elk darter)	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. sp. (greenfin darter)	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
E. (*Ulocentra*) sp.	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E?	—	—
E. (*Ulocentra*) sp.	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—	—	—
E. (*Ulocentra*) sp.	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	M

E. (*Ulocentra*) sp.	—	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	N	—	—	O
E. (*Ulocentra*) sp.	x	x	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
E. sp. (*cragini*-like)	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
Perca flavescens	x	x	—	x	x	—	NI	NI	NI	NI	NI	—	—	NI	NI	NI	—	—	IP	—	—	IP	—	IP	No	M
Percina aurantiaca	—	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
P. burtoni	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
P. c. caprodes	—	x	x	x	x	—	—	—	—	—	—	—	—	—	N	N	N	N	—	N	N	N	N	N	—	M
P. c. semifasciata	—	x	—	x	x	—	—	—	—	—	—	—	—	—	N	—	—	—	—	—	—	—	—	—	No	M
P. copelandi	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	N	N	—	N	—	GM
P. c. crassa	—	x	—	—	x	—	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	So	—
P. c. roanoka	—	x	—	—	x	—	—	—	N	N	N	NI	—	—	—	—	—	—	NI	—	—	—	—	—	—	—
P. e. evides	—	x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	—	N	N	—	N	—	M
P. evides subsp.	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	E	—	—
P. macrocephala	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—	N	N	—	N	—	O
P. maculata	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	N	N	N	N	N	N	—	GM
P. n. notogramma	—	x	—	—	x	—	—	—	—	—	—	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
P. n. montuosa	—	x	—	—	x	—	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. oxyrhyncha	—	x	x	x	x	—	—	—	—	—	—	—	—	—	—	N	N	N	N	—	—	—	—	—	—	O
P. p. peltata	—	x	—	—	x	—	—	—	—	—	—	N	N	N	N	—	—	—	—	—	—	—	—	—	No	—
P. p. nevisense	—	x	—	—	x	—	—	—	N	N	N	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. peltata subsp.	—	x	—	—	x	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. phoxocephala	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—	N	N	—	—	N	N	N	—	N	—	M
P. rex	—	x	—	—	x	—	—	—	—	—	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. s. sciera	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	N	N	—	N	—	GM
P. shumardi	—	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	GM
P. squamata	—	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—
P. uranidea	—	x	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	N	—	GM
Stizostedion canadense	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—	N	N	—	N	—	M
S. v. vitreum	—	x	—	x	x	—	IP	—	NI	—	NI	NI	—	—	I	N	—	N	NI	N	N	N	—	N	—	GM
SCIAENIDAE																										
Aplodinotus grunniens	x	x	—	x	—	—	—	—	—	—	—	—	—	—	—	N	—	N	—	—	N	N	—	N	—	GM

SOURCES AND TREATMENT OF RECORDS.—In addition to the extensive museum collections available to us and our field observations of fishes and their ecology in the area, we have relied heavily, but discriminantly, upon the literature. The pre-1900 literature was important in determining natural ranges. Many of the doubtful records in these and later works were checked when specimens were extant; otherwise certain records were not accepted. Information contributed by current workers was also of much aid.

A selected list of references providing distribution records is given below. In order to conserve space, papers treating a single species, or several, are not listed, even though some were important sources for distributional and ecological data. Studies dealing with the zoögeography and evolution of components of the central Appalachians fish fauna are cited in other sections of this paper.

Central Appalachian drainages: Hubbs and Lagler (1958), Fowler (1945), Rostlund (1952). Neuse drainage: Evermann and Cox (1896), Keup and Bayless (1964). Roanoke drainage: Smith (1893). James drainage: Raney (1950), Flemer and Woolcott (1966). York drainage: Raney and Massmann (1953), Patrick (1961). York and Rappahannock drainages: Massmann, Ladd and McCutcheon (1952). Potomac drainage: Uhler and Lugger (1876), Howden and Mansueti (1951), Ross (1959a). Chesapeake region: Massmann (1954). West Virginia: Evermann and Bollman (1886), Goldsborough and Clark (1908)(Schwartz (ms.). New-Kanawha drainage: Addair (1944), Ross (1959b), Ross and Perkins (1959). Big Sandy drainage: Kirkwood (1957), Turner (1961). Cumberland drainage: Jordan and Swain (1884), Kirsch (1892, 1893), Shoup and Peyton (1940), Shoup, Peyton and Gentry (1941), Krumholz (1958), Turner (1959, 1961), Clay (1962b), Charles (1966), Carter and Jones (1969). Tennessee drainage: Jordan (1889), Gilbert (1891), Evermann and Hildebrand (1916), L. F. Miller (1944), Dendy (1946), Lennon (1962), Ross and Carico (1963), Ramsey (1965), Fitz (1968), Smith-Vaniz (1968), Sisk (1969). Kentucky and/or Tennessee: Jordan and Brayton (1878), Woolman (1892), Evermann (1918), Kuhne (1939), Clay (1962a). North Carolina: Cope (1870), Jordan (1889), Smith (1907), Ratledge, Carnes and Collins (1966). Virginia: Cope (1868), Jordan (1889).

Letter symbols are used in table 1 to categorize the status of freshwater fishes by drainages. The letter "E" indicates that a form is known from only one drainage. An exclusively shared form (table 2) is native to only two drainages (at least one of which is within the region). "N" signifies that there is no doubt that a form is native. "I" indicates a known introduction(s) (transplantation) of a form into a drainage to which it is not regarded as native. Exotic introductions include *Salmo trutta, Carassius auratus, Cyprinus carpio, Leuciscus idus* and *Tinca tinca*. Species known to be transplanted or probably so from North American drainages other than those within the area are *Oncorhynchus nerka kennerleyi, Salmo gairdneri, Esox lucius, Nocomis leptocephalus interocularis, Notropis lutipinnis, Fundulus stellifer, Culaea inconstans* and *Micropterus coosae*. A species may be both native and (later) introduced to a drainage; in such cases the species is regarded as native. Problems concerning introductions were discussed by Lachner, Robins and Courtenay (1970).

The "NP" (probably present, native) category is used few times for species of local occurrence but with a wide distribution in regions beyond the limit of a drainage from which it is presently unknown. Species regarded as NP are: *Lampetra aepyptera* (three drainages), *L. lamottei* (three drainages), *Notropis bifrenatus* (Tar drainage), *Heterandria formosa* (Peedee drainage) and *Enneacanthus chaetodon* (Tar and Roanoke drainages).

"NI" or "IP" designations indicate uncertainty regarding the status of a form, either native or introduced, for several reasons: (1) the native range was not determined early (prior to about 1900); (2) it is a frequently stocked gamefish, such as many centrarchids and the larger ictalurids; (3) it is a widely reared and transported bait fish, as speices of *Pimephales* and *Notemigonus crysoleucas;* (4) it is a hardy species and frequently seined by fisherme nand transported to adjacent drainages fo ruse as bait, as species of *Nocomis* and *Noturus;* (5) it is a species possibly included in hatchery truck shipments of gamefishes. Thus there are numerous opportunities for introduction. In particular, we have data on the capture for the first time of at least six species of minnows and darters in the New River drainage after about 1960, although this drainage was well-surveyed earlier. Similar, but less marked, situations are known for other drainages. It is probable that the records of some of these species resulted from natural population expansion of rare or localized species, or from more intensive collecting efforts. However, we do not believe that all the recent first records are a result of these factors. After careful consideration of the available data bearing on each species, we made a decision to regard some species as probably native (NI) and others as probably introduced (IP), primarily for the purpose of quantifying faunal relationships. Some species that we have regarded as native may be introduced, and vice versa.

Distributional data in tables 1 and 2 are summarized in tables 3 through 6. Distinction Indices (table 6) were calculated for Atlantic slope drainages. The Tar and Neuse drainages, which have very closely related faunas, were regarded as one drainage for this index. Each index consists of the sum of the number of forms reaching their northern or southern range limit within a drainage, added to the number of forms that are endemic to the drainage considered. *Rhinichthys atratulus obtusus, Etheostoma b. blennioides* and *Percina c. caprodes* are the only forms, other than endemics, that occur in only one central Atlantic slope drainage (the Potomac); each contributed a value of 2 to the Potomac Distinction Index. Average Faunal Resemblance Indices were calculated for selected pairs of drainages (table 7) with a formula discussed by Long (1963): Average Faunal Resemblance $= C(N_1 + N_2)$ $100/2N_1N_2$, where $C =$ number of forms common to drainage 1 and 2, and N_1 and $N_2 =$, respectively, the total number of forms in drainages 1 and 2. Distinction Indices are useful in expressing faunal differences based on endem-

TABLE 2—*Species and subspecies exclusively shared by two drainages.*

SANTEE-PEEDEE
- *Hybopsis hypsinotus*
- *Hybopsis labrosa*
- *Notropis analostanus chloristius*
- *Notropis pyrrhomelas*
- *Etheostoma c. collis*

PEEDEE-ROANOKE
- *Notropis chiliticus*

TAR-NEUSE
- *Noturus furiosus*

ROANOKE-JAMES
- *Noturus gilberti*

YORK-RAPPAHANNOCK
- *Etheostoma olmstedi vexillare*

NEW-KANAWHA
- *Etheostoma osburni*

CUMBERLAND-KENTUCKY
- *Etheostoma sagitta*
- *Etheostoma (Ulocentra)* sp.

TENNESSEE-CUMBERLAND
- *Clinostomus funduloides estor*
- *Hybopsis i. insignis*
- *Notropis rubellus micropteryx*
- *Notropis* sp. (paleband shiner)
- *Notropis* sp. (sawfin shiner)
- *Fundulus* sp.
- *Etheostoma cinereum*
- *Etheostoma stigmaeum jessiae*
- *Etheostoma luteovinctum*
- *Etheostoma rufilineatum*
- *Etheostoma (Ulocentra)* sp.
- *Percina burtoni*
- *Percina squamata*

TENNESSEE-MOBILE
- *Notropis bellus*
- *Notropis lirus*
- *Notropis stilbius*

TENNESSEE-SAVANNAH
- *Clinostomus funduloides* subsp.
- *Notropis rubricroceus*

TENNESSEE-NEW
- *Cottus bairdii* subsp.

icity and faunal breaks in a series of drainages. Indices of Faunal Resemblance relate draiange faunas on the basis of the size of faunas and the numbers of shared forms; they may also indicate faunal breaks.

EXTRALIMITAL RANGES.—In the two right-hand columns of table 1 are symbols indicating part of, or the entire, extralimital range of freshwater species and subspecies native to the area: "G" includes at least part of the Gulf of Mexico slope (not including the Mississippi basin); "M" includes at least the lower or central Mississippi basin or both; "O" signifies predominantly or entirely a form of the Ohio basin; "So" forms occur south of the Peedee drainage on the Atlantic slope; "No" forms range north of the Potomac drainage on the Atlantic slope. The extension of some forms into other areas, such as the upper Mississippi and Missouri basins, the Great Lakes-Saint Lawrence basin and the New England region, is not indicated.

HABITAT CATEGORIZATION.—Fishes of central eastern United States form a diverse ecological assemblage, comprising creek to large-river species, and from high gradient, montane forms to lowland and Coastal Plain ones. Different ecological types appear to have somewhat different histories of evolution and dispersal. Fishes are classified by their "typical" habitat, or that which they generally occupy in the area (table 1). We recognize that expatriots and strays may be of zoögeographic significance.

Two physical factors of streams were assessed, gradient and width. A brief discussion of rock types in the area is found in a review by Hack (1969).

TABLE 3—*Number of native and endemic freshwater fishes by family and central Appalachian drainages. (Number of endemic forms in smaller families not indicated by draiange).*

				Atlantic Slope									Ohio Basin								
	Total Native Freshwater	(Total Endemic)	% Endemic	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee
Petromyzontidae	6	(1)	17	—	—	1	1	2	2	2	2	2	1	4	2	—	—	2	4	—	5
Acipenseridae	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	2
Polyodontidae	1	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	1	—	1
Amiidae	1	—	—	1	1	1	1	1	1	1	—	1	—	—	—	—	—	—	—	—	1
Hiodontidae	2	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	1	2	—	2
Salmonidae	1	—	—	—	—	—	—	1	1	—	1	1	1	—	—	1	—	—	—	—	1
Umbridae	1	—	—	1	1	1	1	1	1	1	—	1	—	—	—	—	—	—	—	—	—
Esocidae	4	—	—	2	2	2	2	2	2	2	2	2	1	1	1	—	—	—	2	—	3
Cyprinidae	106	(13)	10	22	19	20	17	23	24	18	16	23	27	15	28	24	16	26	45	14	60
(no. endemic)	.	.	.	(1)	(1)	.	.	.	(1)	.	.	.	.	.	.	(3)	.	.	.	.	(7)
Catostomidae	28	(3)	11	10	8	8	7	14	8	4	4	6	11	8	13	3	7	12	17	5	17
(no. endemic)	.	.	.	.	.	.	.	(3)	.	.	.	.	.	.	.	.	.	.	.	.	.
Ictaluridae	21	(2)	10	7	7	7	6	7	6	5	4	5	8	6	6	3	2	7	13	3	15
(no. endemic)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(2)
Amblyopsidae	3	—	—	1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	2	—	2
Aphredoderidae	1	—	—	1	1	1	1	1	1	1	1	1	—	—	—	—	—	—	1	—	1

TABLE 3—Continued—*Number of native and endemic freshwater fishes by family and central Appalachian drainages. (Number of endemic forms in smaller families not indicated by drainage).*

				Atlantic Slope									Ohio Basin								
	Total Native Freshwater	(Total Endemic)	% Endemic	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee
Percopsidae	1	—	—	—	—	—	—	—	—	—	—	1	1	1	1	—	1	—	—	—	—
Cyprinodontidae	7	(1)	14	2	2	2	1	2	—	—	—	—	—	—	—	—	—	—	4	1	5
Poeciliidae	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Atherinidae	1	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	1	1	1	1
Cottidae	7	(2)	29	—	—	—	—	1	2	—	1	2	1	1	1	3	1	—	1	—	4
Percichthyidae	2	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	—	2
Centrarchidae	25	—	—	16	16	13	13	11	7	7	3	3	9	8	11	3	6	8	13	6	16
Percidae	91	(29)	32	8	7	11	9	16	12	7	7	10	16	13	20	10	10	16	39	8	52
(no. endemic)	.	.	.	(1)	.	.	.	(3)	(2)	.	.	.	.	.	.	(1)	.	.	(6)	(1)	(15)
Sciaenidae	1	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	1	1	—	1

Table 4—*Number of total, introduced, diadromus or euryhaline (marine), native, endemic, and exclusively shared forms in central Appalachian drainages.*

	Atlantic Slope									Ohio Basin								
	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee
Total forms	94	79	84	73	105	87	62	61	91	94	65	98	72	45	80	166	51	215
Introduced	14	5	8	5	14	12	6	12	25	11	4	8	25	1	2	7	13	14
(% of total)	(15)	(6)	(10)	(7)	(13)	(14)	(10)	(20)	(27)	(12)	(6)	(8)	(35)	(2)	(2)	(4)	(25)	(6)
Marine	8	8	8	8	8	8	8	8	8	3	2	4	—	—	4	9	—	10
Native freshwater forms	72	66	68	60	83	67	48	41	58	80	59	86	47	44	74	150	38	191
Endemic	2	1	—	—	6	3	—	—	—	—	—	—	5	—	—	6	1	27
(% of native freshwater forms)	(3)	(2)	.	.	(7)	(4)	.	.	.	.	.	.	(10)	.	.	(4)	(3)	(14)
Exclusively shared	6	—	1	1	2	1	1	1	—	—	—	1	2	—	—	15	2	19
(% of native freshwater farms)	(7)	.	(1)	(2)	(2)	(1)	(2)	(2)	.	.	.	(1)	(4)	.	.	(10)	(5)	(10)

TABLE 5—*Numbers of fishes by families or groups of families and drainage areas in the central Appalachian region.*

Family	Atlantic Slope only	Both drainage areas	Ohio Basin only
Petromyzontidae to Esocidae	2	5	11
Cyprinidae	26	22	58
Catostomidae	9	7	12
Ictaluridae	5	4	12
Amblyopsidae to Percichthyidae, Sciaenidae	5	3	16
Centrarchidae	9	8	8
Percidae	21	8	62
TOTAL (%)	77 (25)	57 (18)	179 (57)

Aquatic vegetation is not considered, for it appears that at least the higher vegetation has little or no direct effect on the distribution of species by drainages. Knowledge of chemical preferences of most species is insufficient to permit a detailed analysis in relation to water chemistry.

GRADIENT.—Lowland species are those of the Atlantic Coastal Plain, the extreme lower portion of the Cumberland and Tennessee drainages, western tributaries of the ascending portion of the Tennessee River and large quiet sections along big rivers. Moderate, occasionally swift, currents may occur in the lowlands, particularly in the zone of the Fall Line. Upland species include, roughly from east to west, those of the Piedmont, Ridge and Valley, western (Appalachian or Cumberland) Plateau provinces, the Highland Rims and the Nashville Basin. The upland category is a broad one; our concept of it is based partly on the presence in major tributaries and smaller streams of riffles, or shoals with a moderate current, constituting, at least, an average of about 5 to 10 percent of the length of the stream. Upland streams west of the Appalachian Divide tend to be more gravelly or rocky than those on the Piedmont, east of the Divide, which tend to be sandy. Montane is the most restricted category; included are the higher gradient streams of the Blue Ridge, Great Smoky and central Allegheny mountains with a riffle-pool ratio of about 1:1.

An Average Gradient Index was calculated for each family (table 8) and for each drainage fauna (table 9) from frequency distributions obtained by assigning a numerical rank, for gradient category(ies) inhabited, to each native freshwater form. Ranks and categories are: 1—lowland; 2—lowland and upland; 3—upland; 4—upland and montane; 5—montane. The total of ranks was divided by the number of forms in the family or drainage to give the index. This index provides an estimate of the average gradient occupied by members of a family or a drainage fauna. It is based on the relative number of forms in each gradient category, but does not indicate the entire range of gradients inhabited. The index utilizes an average rank for forms placed in two categories. For example, a species of upland and montane habitats is ranked as 4; whereas, a strictly montane species is ranked as 5. The formei species may be as common in montane streams as the latter but is ranked lower.

STREAM SIZE.—Creeks are waters which average up to about 30 feet in width; streams average between about 30 and 200 feet in width; rivers are greater than 200 feet in average width.

Many species placed in the river category were also classified arbitrarily as lowland forms, for lack of specific information on their habitat. This ranking may not be valid for river forms that occur in swifter currents. However, for discerning pathways of fish dispersal, we are mainly concerned with whether a form is a big river one, or predominantly a lowland one, and not if it occurs in both habitat types. Stream size categories also tend to break down for species that inhabit lowland, braided streams or pondlike backwater areas. Many species were placed in more than one gradient or stream size category. A category underlined in table 1 indicates that habitat which was obviously most frequented. Ecological classification of species was based on their habitat within the study area. Certain species, such as *Hybopsis aestivalis*, commonly occur in different habitats outside of our study area.

DRAINAGE DESCRIPTIONS

The Peedee drainage heads on the eastern front of the Blue Ridge and has only a very small portion of its drainage in this province; it drains a large area of the Piedmont and Coastal Plain (fig. 1). The Cape Fear, Neuse and Tar drainages are smaller than the Peedee, they originate on the Piedmont, and have a large portion of their basin on the Coastal Plain. The Roanoke drainage proper arises, but has only a very small area, in the Ridge and Valley and Blue Ridge provinces. The Dan River system, the large southern tributary of the Roanoke, begins on the Blue Ridge and enters the Roanoke River on the Piedmont. The Coastal Plain section of the Roanoke proper is somewhat smaller than that of the four drainages considered above. The Chowan system is included herein as a part of the Roanoke drainage, although, as often found in studies of geographical variation of eastern fishes, there is some merit in considering it a separate drainage. It enters the upper portion of Albemarle Sound from the North. The Chowan is formed by three main tributaries, two of which, the Meherrin and Nottoway Rivers, begin on the Piedmont; the third, the Blackwater River, lies entirely on the Coastal Plain. The James and Potomac drainages, of the southwestern Chesapeake basin, have a large portion of their area within the Ridge and Valley and Blue Ridge provinces. The Rappahannock and York drainages are situated between the James

Table 6—*Numbers of range terminations and Distinction Indices of central Atlantic slope drainages (Distinction Index = total range terminations + 1 for each endemic form; range disjunctions not included as terminations).*

Drainage	Family	Range Terminations: SOUTH (from North)	Total	NORTH (from South)	Total	Endemic forms	Distinction Index
Peedee	Cyprinidae	4		4			
	Percidae	1		3			
	other	1	6	—	7	2	15
Cape Fear	Cyprinidae	2		3			
	Catostomidae	—		2			
	Centrarchidae	—		4			
	Percidae	3		2			
	other	—	5	2	13	1	19
Tar-Neuse	Cyprinidae	5		2			
	Catostomidae	1		—			
	Centrarchidae	1		2			
	Percidae	6		—			
	other	2	15	1	5	—	20
Roanoke	Cyprinidae	2		5			
	Catostomidae	2		2			
	Centrarchidae	—		3			
	Percidae	1		3			
	other	3	8	4	17	6	31
James	Cyprinidae	6		5			
	Catostomidae	—		2			
	Centrarchidae	—		1			
	Percidae	2		2			
	other	1	9	1	11	3	23
York	Cyprinidae	—		2			
	Centrarchidae	—		1			
	Percidae	1	1	1	4	—	5
Rappahannock	Cyprinidae	1		—			
	Percidae	—	1	1	1	—	2
Potomac	Cyprinidae	5		1			
	Catostomidae	—		1			
	Percidae	3		2			
	other	1	9	—	4	—	13

TABLE 7—*Number of shared fishes and Average Faunal Resemblance Indices (in parentheses) of central Atlantic slope drainages and selected drainages of the Ohio River basin.*

	Atlantic Slope									Ohio Basin				
	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Kanawha: below falls	Kanawha: above falls	Cumberland: below falls	Cumberland: above falls	Tennessee
Total native freshwater fishes	72	66	68	60	83	67	48	41	58	86	47	150	38	191
Peedee	—	58	47	41	47	29	28	20	26	14	9	17	6	21
		(84)	(67)	(63)	(61)	(42)	(49)	(38)	(40)	(18)	(16)	(18)	(12)	(20)
Cape Fear	—	—	52	45	48	30	28	21	26	13	6	16	5	20
			(78)	(72)	(65)	(45)	(50)	(42)	(42)	(17)	(11)	(17)	(10)	(20)
Neuse	—	—	—	60	63	43	35	25	30	15	13	15	8	21
				(94)	(84)	(64)	(62)	(49)	(48)	(20)	(23)	(16)	(16)	(21)
Tar	—	—	—	—	57	42	35	25	29	16	12	17	8	20
					(82)	(66)	(66)	(51)	(49)	(23)	(23)	(20)	(17)	(22)
Roanoke	—	—	—	—	—	55	39	31	38	19	21	21	10	26
						(74)	(64)	(57)	(56)	(23)	(35)	(20)	(19)	(23)
James	—	—	—	—	—	—	46	37	45	20	21	19	10	26
							(82)	(73)	(72)	(27)	(38)	(21)	(21)	(26)
York	—	—	—	—	—	—	—	35	39	14	11	13	7	16
								(79)	(74)	(23)	(23)	(18)	(17)	(21)
Rappahannock	—	—	—	—	—	—	—	—	40	14	10	11	6	14
									(83)	(25)	(23)	(17)	(15)	(21)
Potomac	—	—	—	—	—	—	—	—	—	23	16	19	12	23
										(33)	(31)	(23)	(26)	(26)
Kanawha: below falls	—	—	—	—	—	—	—	—	—	—	25	75	32	75
											(41)	(69)	(61)	(63)
Kanawha: above falls	—	—	—	—	—	—	—	—	—	—	—	22	17	27
												(31)	(40)	(36)
Cumberland: below falls	—	—	—	—	—	—	—	—	—	—	—	—	36	136
													(59)	(81)
Cumberland: above falls	—	—	—	—	—	—	—	—	—	—	—	—	—	35
														(55)

and Potomac, but only the former drains a small portion of the eastern front of the Blue Ridge. Although these four drainages of the Chesapeake basin have a moderate portion of their area on the Coastal Plain, this area is relatively smaller than that from the Roanoke southward, and much of it is "drowned" by estuarine and freshwater tidal conditions.

The Monongahela drainage, part of the upper Ohio basin, drains largely the Appalachian Plateau. One of the main upper tributaries of the Monongahela (the Cheat River system) and the largest Monongahela tributary on the East (the Youghiogheny River system) arise in the western portion of the Ridge and Valley Province. Drainages of the central Ohio basin treated flow largely through the Appalachian Plateau. The New drainage, regarded as that portion of the New-Kanawha drainage above Kanawha Falls, heads in the Blue Ridge and flows through the Ridge and Valley Province, entering a highly dissected portion of the Appalachian Plateau at approximately the Virginia-West Virginia state line.

TABLE 8—*Gradients inhabited by fishes of central Appalachian drainages and Average Gradient Index for each family. (see page 63 for calculation of index).*

Family	Number of Species or Subspecies					Average Gradient Index
	Lowland	Lowland-Upland	Upland	Upland-Montane	Montane	
Petromyzontidae	—	—	5	—	1	3.3
Acipenseridae	2	—	—	—	—	1.0
Polyodontidae	1	—	—	—	—	1.0
Amiidae	1	—	—	—	—	1.0
Hiodontidae	2	—	—	—	—	2.0
Salmonidae	1	—	—	—	—	1.0
Umbridae	1	—	—	—	—	1.0
Esocidae	2	2	—	—	—	1.5
Cyprinidae	10	19	50	22	5	2.9
Catostomidae	6	10	7	4	1	2.4
Ictaluridae	2	9	9	1	—	2.4
Amblyopsidae	1	1	1	—	—	2.0
Aphredoderidae	1	—	—	—	—	1.0
Percopsidae	—	—	1	—	—	3.0
Cyprinodontidae	1	1	5	—	—	2.6
Poeciliidae	1	—	—	—	—	1.0
Atherinidae	—	—	1	—	—	3.0
Cottidae	—	—	4	2	1	3.6
Percichthyidae	1	1	—	—	—	1.5
Centrarchidae	10	7	7	1	—	2.0
Percidae	6	10	56	15	4	3.0
Sciaenidae	—	1	—	—	—	2.0
TOTALS (%)	48(15)	61(20)	146(47)	45(14)	13(4)	
		252(81)				
	109(35)			58(19)		

Table 9—*Number of native freshwater species and subspecies, tabulated by drainages (percentages in parentheses), inhabiting various gradient categories; and Average Gradient Index for the fauna of each drainage.*

	Atlantic Slope									Ohio Basin								
Gradient Category	Peedee	Cape Fear	Neuse	Tar	Roanoke	James	York	Rappahannock	Potomac	Monongahela	Little Kanawha	Kanawha: below falls	Kanawha: above falls	Guyandot	Big Sandy	Cumberland: below falls	Cumberland: above falls	Tennessee
Lowland	25	24	19	17	16	10	9	3	7	4	1	6	—	—	4	20	—	26
	(35)	(36)	(28)	(28)	(19)	(15)	(19)	(7)	(12)	(5)	(2)	(7)	.	.	(5)	(13)	.	(14)
Lowland-Upland	25	24	22	20	23	15	14	14	16	25	15	26	3	9	21	37	7	38
	(35)	(36)	(32)	(33)	(28)	(22)	(29)	(34)	(28)	(31)	(25)	(30)	(6)	(20)	(28)	(25)	(18)	(20)
Upland	16	14	21	17	32	27	15	14	18	28	26	32	23	22	30	72	18	83
	(22)	(21)	(31)	(28)	(39)	(40)	(31)	(34)	(31)	(35)	(44)	(37)	(49)	(50)	(41)	(48)	(47)	(43)
Upland-Montane	6	4	6	6	11	14	10	9	16	21	17	22	20	13	19	21	13	32
	(8)	(6)	(9)	(10)	(13)	(21)	(21)	(22)	(28)	(26)	(29)	(26)	(43)	(30)	(26)	(14)	(34)	(17)
Montane	—	—	—	—	1	1	—	1	1	2	—	—	1	—	—	—	—	12
	.	.	.	.	(1)	(1)	.	(2)	(2)	(3)	.	.	(2)	.	.	.	.	(6)
Average Gradient Index of Drainage Fauna	2.0	2.0	2.2	2.2	2.5	2.7	2.5	2.8	2.8	2.9	3.0	2.8	3.4	3.1	2.9	2.6	3.2	2.8

The Cumberland drainage and the Clinch-Powell system and the North and Middle Forks of the Holston River of the Tennessee drainage originate in the Ridge and Valley Province. These drainages then flow largely through upland or rolling country of the Appalachian (or Cumberland) Plateau and the Interior Low Plateaus, which include the eastern and western Highland Rims and the Nashville Basin; they enter lowlands of the Ohio basin near the confluence of the Ohio and Mississippi rivers. Major portions of the eastern tributary systems of the Tennessee drainage, from the upper South Fork Holston River southwestward to the Hiwassee system, drain the Blue Ridge Province.

The New-Kanawha and Cumberland drainages have a major waterfall in their main channel, historically affecting fish distribution. The upstream and downstream sections of these drainages are, for the most part, treated separately.

FAUNAL COMPOSITION

The fish fauna of central Appalachian drainages comprises about 277 native freshwater species or, at least, 313 species and subspecies (forms) distributed among 22 families (tables 1, 3, 4). An additional 13 species and the stickleback family Gasterosteidae are introduced; another 13 species and 3 families are diadromous or euryhaline. Of the 313 forms, 51 (16 per cent) are endemic to a single drainage (table 1) and 31 (10 per cent) are exclusively shared by only two drainages (table 2). The native freshwater fauna comprises about one-half of the approximately 500 species known from North America (Miller, 1965: 569).

Ramsey (1965) listed about 300 species native to 6 major drainages of southeastern United States, including the Tennessee. Miller (1959: fig. 1) indicated that 260 species and 13 families occupy the Mississippi basin and nearby drainages of the Gulf slope. Numbers of species and families decrease northward and westward, with 26 species in 6 families in the New England area and northeastward, 112 species in 12 families in the Great Lakes-St. Lawrence basin, 52 species in 10 families north of the Mississippi and Great Lakes basins and 3 to 23 species in 2 to 5 families in various basins west to northwest of the Mississippi basin (Miller, 1959: fig. 1). The faunas of Texas and Mexico are more speciose than that of western North America, but they do not approach the numbers of species of the southern and central portions of the eastern United States. The Central American fauna is partly one of transition between species and families of the northern and southern hemispheres (Myers, 1966; Miller, 1966).

FAUNAL COMPONENTS AND DIVERSITY.—Miller (1965) divided the North American fauna into two general categories: (1) an Old Fauna and (2) a

New Fauna. Included in the Old Fauna from the area are some ancient relics of pre-Tertiary origin, such as the sturgeons (Acipenseridae), paddlefish (Polyodontidae), gars (Lepisosteidae), bowfin (Amiidae) and groups known or presumed to occur first in the early Tertiary, such as the mooneyes (Hiodontidae), mudminnows (Umbridae), troutperch (Percopsidae), pirateperch (Aphredoderidae) and sunfishes (Centrarchidae). These families range from the primitive chondrosteans and holosteans to the advanced perciforms. They are now oligotypic, except for the Centrarchidae which is represented by numerous species in eastern United States (table 1). Included in the Old Fauna are certain suckers (Catostomidae) and catfishes (Ictaluridae) and the larger perches (Percidae). The vast majority of the groups of the Old Fauna are basically inhabitants of lowlands or big rivers.

The New Fauna, whose origin appears to be no earlier than the Miocene (Miller, 1965), includes the majority of the speciose central Appalachian groups, the minnows (Cyprinidae), advanced suckers (most genera of the Catostominae), madtom catfishes (*Noturus* [Taylor, 1969: fig. 5]), killifishes (Cyprinodontidae), sculpins (Cottidae), darters (Percidae: Etheostomatini) and probably some smaller sunfishes, particularly *Lepomis*. Although members of these groups have radiated into most habitat types, the majority occupy uplands.

Five families, all of which are at least partly included in the New Fauna, are dominant — three ostariophysans, the Cyprinidae, Catostomidae and Ictaluridae, and two perciforms, the Centrarchidae and Percidae (table 3). These comprise 271 (87 per cent) of the 313 native freshwater forms and 47 of the 51 endemic forms. Two additional endemics are sculpins, genus *Cottus*, a group that has radiated in the Appalachian region (Robins, 1961; Williams, 1968; Williams and Robins, 1970) although probably to a lesser extent than in western North America (Robins and Miller, 1957; Bailey and Bond, 1963). A non-parasitic lamprey, genus *Ichthyomyzon* (Raney, 1952), and a cyprinodontid. genus *Fundulus*, are the remaining endemics. It is notable that the Centrarchidae, although a diverse family, apparently lacks endemic and exclusively shared species (an *Elassoma* may be an exception).

The vast majority of the 313 forms inhabit uplands (table 8). Only 48 forms (15 per cent) are considered to be exclusively lowland types; some of the big river inhabitants, so classified by us, may be more properly regarded as upland forms. An additional 61 (20 per cent) are in both upland and lowland habitats. Entirely upland forms number 146 (47 per cent), and upland and montane forms include an additional 45 (14 per cent). Partly or entirely upland forms number 252 (81 per cent). Only 13 (4 per cent) of the 313 species and subspecies are classified as strictly montane inhabitants. Of the five most speciose families, the Centrarchidae has the lowest Average Gradient Index (2.0). Although subspecies of most centrarchids were not treated, it is notable that one of the more upland-dwelling species, *Lepomis megalotis,* is probably the most polytypic in the family (Bailey, 1938).

Elements of the fauna with a limited range, the endemic and exclusively shared forms, belong almost entirely to the upland fauna. Only one of the 51 endemics, *Semotilus* sp., an undescribed cyprinid, is ranked as an entirely lowland species; this habitat categorization may change when more is known of its distribution. The percid, *Etheostoma mariae,* is the only endemic placed in the lowland-upland category. None of the 31 forms exclusively sharing two drainages is regarded as strictly a lowland fish; only two, the Carolina madtom, *Noturus furiosus,* and the Carolina darter, *Etheostoma c. collis,* occupy both lowlands and uplands. Montane inhabitants of limited distribution are more numerous than those of lowlands. Six endemics (but no exclusively shared forms) are strictly montane fishes, and 6 endemics and 3 exclusively shared forms occur in montane and upland situations.

Numbers of species and subspecies occupying each category of stream gradient correspond roughly to the proportion of habitat of each category within the region. Upland waters comprise the major proportion of the habitats and montane streams the least; lowland habitats are somewhat intermediate. The abundance of upland species and subspecies may suggest that such habitats generally provide the most favorable conditions for occupation or speciation of eastern freshwater fishes. Factors, in addition to small drainage area, that possibly contribute to the relatively depauperate nature of the montane fauna may be the rigors of adaptation to swift streams (Hubbs. 1941). The relative scarcity of large streams and rivers in central Appalachian montane districts partially impedes large-river species from entering these districts. Nontidal lowland waters, particularly in the southern United States, generally may have afforded the most constant conditions for aquatic life (excluding spring-runs and subterranean streams), a factor probably involved in survival of relict groups in lowlands. Eastern lowland waters have probably lacked a history of high turbidity when compared to that of streams in the Great Plains; eastern lowland faunas are generally richer than plains faunas, and their components are generally less specialized than plains fishes (adaptations to turbid waters are discussed by Hubbs, 1941; Moore, 1950; Metcalf, 1966).

DIVERSITY BY BASINS

The southern Ohio basin contains 20 of the 22 families in the region (table 3). The two not recorded are Umbridae and Poeciliidae. The central mudminnow, *Umbra limi,* is widely distributed in the northern Ohio basin and may extend into western fringes of the region. The Poeciliidae, represented by the mosquitofish, *Gambusia a. affinis,* does occur in the southern Ohio basin, but this subspecies is regarded as euryhaline. Families with freshwater members on the central Atlantic slope number 16. Atherinids are represented by the brook silverside, *Labidesthes sicculus,* on the south Atlantic slope. Acipenserids (sturgeons) and percichthyids (temperate basses) are native, but anadromous or euryhaline, on the Atlantic slope. The Polyodontidae, Hiodontidae and Sciaenidae, absent from the Atlantic slope, contribute a total of only four species to the North American freshwater fauna.

The importance of the Atlantic slope-Ohio basin divide is more obvious when numbers of species and subspecies are considered. A richer fauna occurs in the Ohio basin; it has 179 forms (57 per cent of the 313 forms) that are absent from the central Atlantic slope, compared with 77 forms (25 per cent) on the Atlantic slope not found in the Ohio basin (table 5). Only 57 forms (18 per cent) occur on both sides of the divide in the region.

All speciose families, except perhaps the Centrarchidae, have a greater numerical diversity in the Ohio basin than on the Atlantic slope. Most fishes of restricted distribution occur in the Ohio basin: 39 (76 percent) of the 51 endemics (tables 3, 4) and 22 (71 per cent) of 31 exclusively shared forms (table 2). No forms are exclusively shared within the area by an Ohio basin or Atlantic slope drainage.

DIVERSITY BY DRAINAGE

ATLANTIC SLOPE.—Diversity of faunas by drainage tends to decrease from the Peedee drainage northward to the Tar drainage, from 72 forms to 60; but it increases to a peak of 83 in the Roanoke drainage (table 4). The Roanoke has the richest fauna on the Atlantic slope of the United States; slightly less diverse faunas occupy major south Atlantic slope drainages, the Savannah and Santee (Ramsey, ms.). Numbers of forms decline north of the Roanoke, from 67 in the James to 41 in the Rapphannock, and then increase to 58 in the Potomac. Endemic fishes are found in the Roanoke (six), James (three), Peedee (two) and Cape Fear (one); the percentage of endemic forms in the Roanoke (7 per cent) is the third highest of the region. On the south Atlantic slope, the greatest number of endemics (four) occurs in the Santee drainage (Ramsey, ms.). The Peedee is notable in having six exclusively shared forms; other central Atlantic slope drainages have one or two such forms, or none (table 2).

Families tending toward reduction in numbers northward on the Atlantic slope are the Catostomidae, Ictaluridae, Cyprinodontidae and Centrarchidae (table 3). No major family clearly declines in number of species southward; although minor ones, as the lampreys, Petromyzontidae, the Salmonidae (represented by the brook trout) and the sculpins, Cottidae, show reductions or are absent southward. Families reaching a peak in number of species, or nearly so, in the Roanoke are the Cyprinidae, Catostomidae and Percidae.

A peak in number of forms terminating their distribution southward on the Atlantic slope, from more northerly drainages, occurs in the James (9 forms) and Tar-Neuse drainages (15 forms) (table 6). All of the northern forms terminating in the James are upland fishes and, except possibly *Cottus cognatus*, are widespread in the Chesapeake basin. The peak in the Tar-Neuse is formed largely by upland inhabitants from the Roanoke fauna; thus, the number of forms with their southern limits in the Roanoke is reduced by its contributions to the Tar and Neuse faunas. A peak of forms terminating northward on the Atlantic slope occurs in the Cape Fear (13 forms) and Roanoke drainages (17). The major contribution to the Cape Fear peak is by southern lowland fishes, whereas the high number in the Roanoke represents a mixture of upland and lowland fishes. The third highest peak of forms (11) with northern limits occurs in the James drainage, and is largely related to the presence of characteristic fishes of the Roanoke.

The Roanoke drainage has the most unique fauna on the Atlantic slope, based on a combination of total species and subspecies, numbers of endemic, exclusively shared, and other forms with a limited range, and numbers of range terminations therein — despite its numerous contributions to the Tar, Neuse and James faunas — it has a Distinction Index of 31 (table 6). South- and mid-central Atlantic slope drainages adjacent to the Roanoke have high to intermediate Distinction Indices: James 23, Tar-Neuse 20, Cape Fear 19, Peedee 15. Low indices are characteristic of faunas of drainages on the north-central Atlantic slope (and those more northerly): York 5, Rappahannock 2, Potomac 13.

OHIO BASIN.—The highly speciose faunas of drainages within the Ohio basin (table 3) are in its southern portion, the Tennessee with 191 forms and the Cumberland with 150 forms. There is a depauperacy of faunas above major waterfalls, 47 forms in the New drainage (New-Kanawha drainage above Kanawha Falls) and 38 forms in the upper Cumberland drainage (above Cumberland Falls). Smaller faunas occur above the falls of the Little Kanawha and Cheat rivers. The average size of the faunas in five Ohio basin drainages upstream from the Cumberland (69 forms, range 44 to 86) is slightly higher than that of the central Atlantic slope faunas (63 forms, 41 to 83). Total numbers of forms known from the Monongahela and Guyandot drainages may increase with additional collections from their large rivers and with pollution abatement. An improvement of water quality in the upper Ohio River was accompanied by a rapid increase in the variety and abundance of fishes (Krumholz and Minckley, 1964). There are 112 forms within the Little Kanawha, Kanawha, Guyandot and Big Sandy drainages, [south-central Ohio basin]. The sum rises to 118 by inclusion of the following big river or lowland fishes recorded by Trautman (1957) from the Ohio River between the mouths of the Big Sandy and Little Kanawha: *Acipenser fulvescens Scaphirhynchus platorhynchus, Hiodon tergisus, Esox americans vermiculatus* (from an Ohio tributary), *Cycleptus elongatus* and *Ammocrypta asprella.* Numbers of species and subspecies in the south-central Ohio basin are much less than those of the Tennessee and Cumberland drainage. The latter two harbor a total of at least 205 forms; additional forms possibly present in the lower portion of one or both of these drainages, based on distributions in southeastern Missouri (Pflieger, 1971 [Addendum]), southern Illinois (Smith, 1965) and/or Indiana (Gerking, 1945), are *Ichthyomyzon unicuspis Umbra limi, Notropis lutrensis, N. v. venustus, Erimyzon sucetta, Fundulus Notti dispar, Lepomis symmetricus, Etheostoma asprigene* and *E. microperca.* All of the larger families have more forms in the southwestern portion of the Ohio basin than in its south-central and upper portions.

The faunas of the southwestern Ohio basin are also marked by numerous endemic and exclusively shared form (tables 2, 3). Of 39 Ohio basin endemics. 27 inhabit the Tennessee, and 7 the Cumberland (1 largerly above its falls) — the other 5 endemics are in the New drainage. Of 22 exclusively shared forms in the Ohio basin, the Tennessee has 19, the Cumberland 15, the New 2, and the Kanawha 1. The fauna of the Tennessee drainage is the richest, and includes more endemics than any other North American drainage. Except for the New-Kanawha drainage, endemic and exclusively shared forms are absent from faunas of the south-central and upper portions of the Ohio basin. These faunas are more closely related to those of the northern Ohio basin than to those of the southwestern sector.

Several factors appear to influence numerical diversity of faunas. A correlation exists between size of drainage and numbers of species and subspecies. The largest drainages within the area, the Tennessee and Cumberland (fig. 1), have the richest faunas (table 4). Smaller drainages, the York, Rappahannock, Guyandot, New and upper Cumberland have the fewest forms. A similar relationship was found in drainages of Portugal by Daget (1968). However, the relationship between drainage area and number of species is only a general one. An example of discordancy is that the Cumberland (below its falls) and Roanoke drainages are fairly similar in size but the former has nearly double the number of species.

Diversity and abundance of habitats greatly influence the number of species. These factors are associated with drainage size and number of physiographic and biotic provinces. The large extent of Coastal Plain habitat available from the Cape Fear to the Roanoke permitted development of fairly rich lowland faunas, compared with drainages of the Chesapeake Bay basin, where freshwater Coastal Plain habitat is limited. A general increase in Average Gradient Indices northward on the Atlantic slope (table 9) probably reflects, in part, the northward decrease of Coastal Plain faunas. Centrarchid distribution on the central Atlantic slope (table 3) best demonstrates reduction of lowland fishes northward, since this family has the lowest Average Gradient Index among larger families (table 8). The Tennessee and Cumberland are the only drainages of the Ohio basin in the region with a portion of their hydrography, although small, below or adjacent to the Fall Line; their faunas include a proportionately larger number of strictly lowland fishes than those of the south-central and upper Ohio basins (table 9). Faunas particularly limited by lack of lowland habitat are those above major waterfalls, in the New and upper Cumberland drainages. Montane habitat also influences the number of species. Most montane fishes occur in the upper Tennessee drainage, which has a greater mileage of montane streams than the other drainages studied. Conversely, faunas depauperate in montane fishes are those lacking, or having little, montane habitat, such as those of the south-central Atlantic slope and the York, Little Kanawha, Guyandot, Big Sandy and Cumberland drainages.

A tendency for larger streams to support more species is generally noted in studies of longitudinal distribution of fishes within tributary systems. Several recent studies of this nature were cited by Sheldon (1968). It is unlikely, however, that stream size is a major limiting factor of faunal size of drainages in the region. All of the drainages include at least one big river, seemingly of sufficient width to support all, or nearly all, species within the region that prefer such a habitat. It is implicit that conditions of depth and substrate preferred by the river species are present.

Size of certain faunas and phyletic relationships of some of their fishes indicate that historical factors may be more significant determinants of numerical diveristy and composition than size of drainages. For example, the Tar drainage is smaller but has a distinctly richer fauna than either the New or upper Cumberland drainages. Many elements of the rich upland fauna of the Roanoke drainage are more closely related to species of the Ohio basin than to Atlantic slope forms. Historical factors discussed in following sections are drainage history, routes of dispersal, distance between drainages and their proximity to rich faunas, physiographic and ecologic barriers and effects of past climates.

Means of Dispersal and Drainage History

Important means of traversing drainage divides and pre-Holocene drainage patterns are outlined in this section. Their bearing on specific problems is treated in the following accounts of the faunas of individual drainages.

Interconnecting Rivers—A chief pathway for dispersal between drainages is through rivers that presently connect their mouths, or did so in the past. An extant example is the Ohio River, which joins all of its tributary drainages to form the Ohio basin. The Ohio River was once a shorter stream. Its present upper portion, the Allegheny and Monongahela drainages, flowed northward and formed part of the pre-Pleistocene Laurentian River basin, which drained a major portion of the Great Lakes region. The present middle and lower Ohio basin was part of the vast Teays River basin, a precursor of the eastern part of the Mississippi basin. Present drainage relations in the Ohio basin resulted largely from effects of Pleistocene glaciation. The upper Teays is represented by the New-Kanawha drainage. A good semipopular account of the Teays basin was given by Janssen (1953); major studies on which the account was based were included in his bibliography. An illustration of the Teays and parts of adjacent basins is given by Lachner and Jenkins (1971a). The Teays (early eastern Mississippi) basin was probably a major center of evolution and dispersal.

Interdrainage connections on the central Atlantic slope were the Greater Susquehanna River (interconnecting all present, separate Chesapeake Bay drainages), the Greater Roanoke River (connecting the Roanoke and Chowan rivers) and probably the Greater Pamlico River (joining the Tar and Neuse rivers) (fig. 1; Darton, 1894; Shattuck, 1906; 134, pl. 31; Lachner and Jenkins, 1971a). During Pleistocene times of lower sea level, these large rivers drained lands that are now part of the Continental Shelf. Estimates of eustatic changes in sea level were summarized by Curray (1965) and Stearns (1969). The Continental Shelf also apparently provided suitable smaller stream habitat for lowland freshwater fishes, as indicated in studies by Frankel and Thomas (1966), Emery, Wigley and Rubin (1966), and those of fishes by Cole (1967) and Jenkins and Zorach (1970).

While large rivers such as the Greater Susquehanna have been invoked, with much justification, as major freshwater dispers all routes (Bailey, 1945), their importance may be overestimated for species that prefer small, clear streams. Large rivers may have been (and remain) generally unsuited for such species because of size, high turbidity and sediment levels. However, local concentrations of islands in large rivers may have ameliorative effects, enabling rivers to serve more effectively as filter bridges for stream fishes. A group of islands may produce small, swift channels and backwaters. Typically stream-inhabiting species then may be represented by stable populations rather than waifs. (Observations by one of us [Jenkins] have revealed that elements of stream faunas occur, and some reproduce, in the shelter of islands in the Thousand Islands area of the vast St. Lawrence River.)

STREAM CAPTURE.—A list of stream piracies between drainages is given below; references to captures between tributaries within the same drainage are omitted. Geological evidence given by authors for each capture varies from general statements to detailed analyses. Although some captures were detected by earlier workers whose concepts of Appalachian erosion now seem partly unfounded, such as aspects of a concept of peneplane-erosion cycles (criticized by Thompson, 1939:1324, 1328-1330; Dietrich, 1959:29-30, 51-54; Hack. 1969:3-5), the probability that those captures listed did occur seems, in at least most cases, to have been unaltered.

Peedee-New (Wright, 1931:246); Peedee-Santee (White, 1953); Peedee-Roanoke (Weaver, 1897; White, 1953); Roanoke-Neuse-Tar (Lachner and Jenkins, 1971a); Roanoke-New (Wright, 1934:61-67; Thompson, 1939:1333, 1353; Dietrich, 1959:20-23, 29, 32, 34; Ross, 1969); Roanoke-James (Wright, 1934:62-63; Ross, 1969); James-New (Wright, 1934:68; Thompson, 1939:1352-1353); James-Rappahannock (Watson and Cline, 1913); James-Potomac (Thompson, 1939:1349-1351; Ross, 1969); Rappahannock-Potomac (Watson and Cline, 1913; Thompson, 1939:1346-1350); Potomac-Susquehanna (Ross, 1952:88); Potomac-Monongahela (Ross, 1958b; Schwartz, 1965); New-Monongahela (Fridley, 1933; Wright, 1934:55); New-Kanawha (Campbell, 1896:669-670); Cumberland-Kentucky, (Campbell, 1896:671; Sauer, 1927:27, Kuehne and Bailey, 1961); Cumberland-Green (Sauer, 1927:27); Tennessee-New (Ross and Carico, 1963:7-10); Tennessee—certain adjacent drainages (Ross, ms. [not indicated in our fig. 1]).

Most combinations (pairs) of adjacent drainages in the central Appalachians yield geological evidence of at least one stream capture; sites (theaters) of these captures are indicated in figure 1. Additional or multiple captures may have occurred, some between drainage pairs not listed above. Wright (1936: 246) and Thompson (1939:1353) pointed out that evidence of capture disappears with active dissection of the capture area. Thompson (1939) seemed to imply that more captures were detected in the central Appalachians than documented in his paper. Dietrich (1959:32) stated that piracy is considered to be common near highly asymetric divides, for example the Roanoke-New drainage divide. Hack (1969:7, 9, 12) regarded captures to be of frequent occurrence. Most recognized theaters of capture are in montane regions and higher elevations of upland regions. It is possible that captures were frequent in readily eroded terrain on the lower Piedmont and Coastal Plain, where lateral meandering would be appreciable. Lack of published evidence for such captures between pairs of drainages does not justify an assumption that they did not occur. Opportunity for development of a comparatively similar fauna in all central Appalachian drainages could have existed. Differences among faunas relate to various characteristics of captures, different ecologies and the age of the extant fauna.

Size of streams involved in piracy is probably an important determinant of their utilization by different species. Hack (1969:11) stated that "Captures of large drainage basins are rare." Thus, species preferring creeks and small streams are probably those most likely to have traversed divides. Large river fishes native only to the Ohio basin (in the region), such as *Cycleptus elongatus*, species of *Ictiobus* and most of *Carpiodes, Ictalurus furcatus, Pylodictis olivaris* and *Aplodinotus grunniens*, would tend not to utilize smaller stream captures on the Atlantic-Ohio divide. Other ecological requirements, if not met in a theater of piracy, or in that portion of the captured stream above the theater, would also militate against divide transgression. Species limited to habitats on the Coastal Plain or Ohio valley lowlands would have little opportunity to gain access to captures on the Atlantic-Ohio divide. Exchange of such species, particularly centrarchids, between the central Atlantic slope and Ohio basin would more likely result by their utilization of a more southerly route, consisting partly of drainage connections on lowlands of the Gulf slope. Possible faunal saturation and interspecific competition are additional factors for consideration in attempting to determine why certain species are absent from drainages to which they probably had access and in which their preferred habitat seems to exist. Of these two factors, insufficient information directly relevant to fishes in the area is known

The general deficiency or uncertainty of data in regard to dating captures presents a problem in their usage to explain fish distribution. Thompson (1939:1353) stated that "Captures that can now be definitely recognized belong to comparatively recent geological time." Ross (1969:285) assumed that many piracies between the Roanoke and New drainages transpired during Wisconsin time. A problem associated with distributional studies is the lack of information on the age of species and subspecies; those whose origin postdates a capture could not have utilized that capture. Certainly, most members of the Old Fauna were potentially able to use the captures listed above, if suitable ecological conditions were present. The fossil record, however, has yielded little data bearing directly on evolution and dispersal of eastern American freshwater fishes. Most live in areas of erosion, with fewer chances of fossilization than in areas of deposition. Uyeno and Miller (1963) and Miller (1965) critically reviewed the fossil record of American freshwater fishes. Only two fossil sites are in drainages of the central Appalachians; these were dated as possibly of Miocene age and contained remains of the primitive garfish genus *Lepisosteus*. It is possible that many species and subspecies, particularly of cyprinids, redhorse suckers (*Moxostoma*) and their allies, madtom catfishes (Taylor, 1969: 220, fig. 5) and darters (*Etheostomatini*), originated during late Pleistocene and Recent times in eastern North America. "Explosive" speciation of fishes has occurred in other regions, particularly the Rift Valley lakes of Africa (Greenwood, 1964), Lake Lanao in the Phillippines (Myers, 1960) and in other areas noted by Myers. Many of the recently evolved central Appalachian forms, although they have not been identified, may have had no opportunity to utilize some of the more recent captures. Hydrographic and taxonomic data summarized by Miller (1961) indicate a wide range of evolutionary rates in freshwater fishes of western North America, with some forms differentiating since the Pleistocene.

Events during capture bear on the predominant direction of faunal exchange across the Atlantic slope-Ohio basin divide and on identification of major centers of evolution. As a result of piracy, an entire section of a drainage is diverted into its captor, involving transferal of the typical inhabitants of the captured stream and possibly strays or migrants of species occurring downstream. Volume of flow of the captured stream at the time of surface piracy may, however, be reduced in some cases by preceding piracy of ground water (Mackin, 1933:326), thus possibly effecting withdrawal of some species from the captured section prior to surface piracy. With or without subsurface piracy, the captured stream probably receives a smaller number of species than it delivers to the captor, unless the fauna of the former is highly depauperate; its potential entrants can gain access generally only from the area of capture. The Atlantic-Ohio divide has migrated westward; Atlantic slope streams generally were the captors (Thompson, 1939; Hack, 1969; Ross, 1969). Thus, faunas of south and central Atlantic slope drainages would have tended to become more enriched by capture than those of the adjacent drainages of the Ohio basin, for example the Tennessee. The Tennessee fauna is much richer than that of adjacent Atlantic slope drainages and this is evidence that many of its fishes are autochthonous or that they originated elsewhere in the Mississippi basin rather than on the Atlantic slope. An additional factor contributing to the great difference between the Tennessee and Atlantic slope drainages in the number of species is that only montane streams of the Tennessee head on the Atlantic-Ohio divide; these streams have fewer species to contribute to the Atlantic slope than do those of lower elevations in the Tennessee.

Some workers have attempted to identify the site of first entry by capture of a species to a drainage, primarily on the basis of its present occurrence in one or a few tributaries of the drainage (Lachner and Jenkins, 1971a), or when the site is traceable to a small area (Schwartz, 1965). Such distribution patterns are uncommon. The possibility of multiple capture and the existence of modifiers of distribution, such as change of ecological conditions and interspecific competition, indicate that even the most suggestive evidence of the site of drainage entry may lead to invalid conclusions. Another difficulty in determining sites of drainage entry is that limited distribution may result from introduction rather than from natural factors.

Capture between two tributary systems of the same drainage (intradrainage capture or autopiracy) probably has less significance for the origin of species than interdrainage capture. Intradrainage capture would provide genetic isolation if, for example, a population of a montane species becomes segregated into two systems that join in lowlands. Frequent and widespread intradrainage capture would effect a wide distribution of many species within a drainage.

Effects of the Pleistocene.—Drainage and climatic changes associated with Pleistocene glaciation had major effects on the distribution and evolution of the North American fish fauna. Although the central Appalachian region was not glaciated—except possibly for small, local glaciers at high elevations — certain aspects of its drainage history may be traced to glaciation. Extended rivers (for example, the Greater Susquehanna River) and, probably, a high frequency of stream capture (Ross, 1969: 285-286), because of greater flow and erosive competence, were effects of glacial, pluvial times. Evidence of increased runoff and river activity in the region during glacial periods was summarized by Schumm (1965). More striking glacial effects north of the region were the development of the Great Lakes basin and their several, temporary, outlets and other major routes of redispersal into the glaciated region (summarized by, among others, Hough, 1963; Hubbs and Lagler, 1958; Greene, 1935; Radforth, 1944; Gerking, 1945; Underhill, 1957; Bailey and Allum, 1962). Results of northern Pleistocene events directly relevant to this study were displacement of many stocks southward into refugia and, with deglaciation, temporary routes were provided into the Appalachian region. Notable among the latter routes was the Horseheads Outlet (Bailey, 1945), from the Lake Ontario drainage into the Greater Susquehanna (if these were contemporaneous), and a pathway involving stream capture from the Lake Erie drainage to the Allegheny drainage (Ross, 1958a: 17-18; Lachner and Jenkins, 1971a), thence to the Monongahela drainage.

The Pleistocene probably retarded evolution of some fishes and hastened that of others. Retardation would have resulted if separated stocks of a species in the process of differentiation became genetically fused with southward displacement, by glaciers or climate, of the northern stock. Such a pattern of gene flow is likely to have occurred, in the East, into the Greater Susquehanna River and its constituent drainages and, in the southern Ohio basin, into drainages of north-central and northeastern Kentucky, West Virginia and into the Monongahela and Allegheny drainages. The paucity or absence of endemic forms or forms of limited total distribution in these drainages is evidence of gene flow southward.

During deglaciation, extended coastal rivers were replaced by marine or estuarine conditions, effecting isolation of populations in previously inter-connected drainages. It has become apparent that colder climatic (and water) temperatures existed during glaciation well south of periglacial areas, at least into the region of central Appalachian drainages (see, among many studies reported in *The Quaternary of the United States,* Whitehead, 1965). Such conditions would have permitted populations of cool-water species to exist at lower elevations than at present and probably increased chances of their spread into tributary systems and springs of a drainage through inter-connecting rivers that are presently uninhabitable. Increased temperatures since the Pleistocene would tend to restrict cooler-water inhabiting fishes to higher altitudes and springs, effecting disjunct or relict populations and opportunities for speciation.

Examples of cool-water forms with a relict or semi-relict population(s) in the area, and the drainages they inhabit are *Salvelinus fontinalis* (Roanoke, Tennessee and southward), *Clinostomus elongatus* (upper Monongahela), *Notropis heterolepis* (lower portion of middle Cumberland), *Semotilus m. margarita* (Potomac), *Catostomus catostomus* (Monongahela), *Percopsis omiscomaycus* (Potomac, Monongahela, Little Kanawha, Kanawha and Guyandot), *Cottus bairdi* subsp. (New, Tennessee), probably other cottids and *Percina caprodes semifasciata* (Potomac). The northern cyprinid *Chrosomus eos* was once reported long ago (Uhler and Lugger, 1876) from the Potomac drainage and the Patapsco (northwestern Chesapeake Bay basin) drainage; these records are either unconfirmed or represent young specimens of *Clinostomus funduloides* (Schwartz, 1963). The relict popualtions and subpopulations of the above species do not appear to have differentiated to a recognizeable extent.

Evidence for extirpation of populations in the New and upper Cumberland drainage because of glacial climatic regimes is discussed below.

Composition and Origin of Drainage Faunas

Peedee Fauna.—The Peedee fauna consists largely of Coastal Plain and Piedmont forms; a very small extent of montane habitat is found in the Peedee drainage. Closest relationships of the fauna are with adjacent faunas to the south and north, respectively, the Santee (Average Faunal Resemblance about 83) and Cape Fear (84; table 7). Both Peedee endemics, *Semotilus* sp. and *Etheostoma mariae*, are Coastal Plain inhabitants; the former possibly occurs in the Cape Fear drainage. *Etheostoma mariae* was first thought (Fowler, 1947) to occur in the Cape Fear drainage, but Richards (1963) indicated its restriction to the Peedee. Five of the six exclusively shared forms in the Peedee are shared with the Santee, the other with the Roanoke (table 2). Distinctive upland fishes of the Roanoke fauna are absent from the Peedee; the similarities between these faunas are based largely on their lowland constituents. Forms with the northern end of their range, on the Atlantic slope, in the Peedee are *Hybopsis hypsinotus, H. labrosa, Notropis analostanus chloristius* (as intergrades with *N. a. analostanus* [Gibbs, 1963]), *Notropis pyrrhomelas, Etheostoma c. collis, E. fusiforme barratti* (Collette, 1962) and *E. flabellare brevispinna* (Ross, in Ross and Carico, 1963). Species with southern range terminations, from more northerly drainages, are *Notropis alborus* (Hubbs and Raney, 1947), *Notropis a. analostanus, N. chiliticus, Fundulus d. diaphanus* (Hubbs and Raney, 1946:14) and probably *Perca flavescens* (Hubbs and Lagler, 1958: 106; Menhinick, Burton and Bailey, ms.).

Cape Fear Fauna.—The Cape Fear, with an absence of montane and typically swift high-upland streams, has only a Piedmont and Coastal Plain fauna. The absence of *Hypentelium nigricans* is notable, as this widespread upland and montane species occurs in all major adjacent drainages. Two upland species, *Catostomus c. commersonii* and *Etheostoma f. flabellare,* are rare. A third, *Notropis cerasinus,* known from one locality in the upper Cape Fear, may have been introduced. The single endemic, *Notropis* sp., occurs on the Piedmont (F. F. Snelson, Jr., pers. comm.). Exclusively shared forms are absent. The Cape Fear fauna is somewhat more closely related to that of the Peedee (Average Faunal Resemblance 84) than to that of the Neuse to its North (78). The break between the faunas of the Cape Fear and Neuse is one of the sharpest on the Atlantic slope. It is effected by 13 forms having the northern end of their range in the Cape Fear and 15 forms with their southern terminus in the Neuse; the total (28) of these is two greater than the number of forms (26) comprising the break between the Roanoke and James drainages (table 6). The 13 fishes with northern limits in the Cape Fear are largely lowlands forms: *Notropis maculatus, N. petersoni, N. scepticus, Minytrema melanops, Moxostoma robustum* (Robins and Raney, 1956), *Ictalurus brunneus* (Yerger and Relyea, 1968), *Heterandria formosa, Elassoma evergladei, Lepomis macrochirus, L. microlophus, L. punctatus, Etheostoma olmstedi maculaticeps* (Cole, 1967) and *Percina c. crassa.* Some of these species occur in small, entirely Coastal Plain drainages between the Cape Fear and Neuse (Ratledge *et al.,* 1966). The break between the Cape Fear and Neuse faunas is accentuated by the absence from the former of 15 forms in the Neuse that are of Roanoke drainage derivation or that probably used the Roanoke as a center of dispersal on the Atlantic slope (see below). Cole (1967:49) noted the biogeographical boundary between the Cape Fear and Neuse, but indicated an absence of known stream exchanges between these drainages. However, from basic similarities between these faunas, it appears that routes of dispersal between the Cape Fear and Neuse existed in the past. The five forms that terminate southward in the Cape Fear, *Notropis albeolus* (Gilbert, 1964), *N. amoenus* (Snelson, 1968), *Etheostoma collis lepidinion, E. f. fusiforme* (Collette, 1962) and *E. f. flabellare,* may have entered this drainage from the Neuse or Roanoke drainages.

NEUSE AND TAR FAUNAS.—These faunas, essentially of Piedmont and Coastal Plain fishes, are the most closely related of all in the region (Average Faunal Resemblance, 94). Their great similarity probably relates to exchange of species by lateral captures, through movements in the Greater Pamlico River and to their reciprocal enrichment with members of the Roanoke fauna. Few forms are limited to the Neuse-Tar group. The only species exclusively shared by these drainages, *Noturus furiosus,* may be found in the Roanoke drainage when its Piedmont and Coastal Plain streams are better collected; it is a relict form (Taylor, 1969:167-169) whose ancestor probably arrived from the Teays via the Roanoke drainage. The Neuse and Tar populations of *Etheostoma nigrum* have differentiated significantly from that of the upper Roanoke (Cole, 1958; this volume). *Percina peltata nevisense* is known with certainty only from the Neuse and Tar, but the population of the Chowan system of the lower Roanoke drainage appears more closely related to it than to the *Percina peltata*-like form of the upper Roanoke (Raney and Suttkus, 1948); the Chowan population is arbitrarily regarded herein as *P. peltata nevisense.* The Neuse-Tar stock of *Notropis ardens,* known as *Notropis matutinus,* may be unworthy of nomenclatural recognition (F. F. Snelson, Jr., pers. comm.).

The Neuse harbors eight species that are apparently absent from the Tar: *Notropis alborus, N. c. cummingsae, N. niveus* (first three, Menhinick, *et al.*, ms.), *Erimyzon sucetta, Ictalurus platycephalus, Fundulus rathbuni* (Brown, 1955), *Etheostoma collis lepidinion, Stizostedion v. vitreum.* All forms found in the Tar occur in the Neuse. Since most of the eight species that are absent from the Tar are typical Coastal Plain or lower Piedmont forms or both, and the richer Neuse fauna lies south of the Tar, it appears that portions of the Neuse lowland fauna have had insufficient opportunity to reach the Tar. The presence of Coastal Plain species in the Neuse, and their absence from the Tar, suggest that their entry into the lower Neuse postdates a late Pleistocene Greater Pamlico route, or that this route was not utilized by some species owing to ecological intolerances. The occurrence of the majority of the above eight forms in the Neuse, Roanoke and Cape Fear drainages, and the geographic relationships of these drainages (fig. 1), indicate that the Tar was circumvented during some major events of faunal interchange. Species having the northeastern end of their range in the Tar are Coastal Plain species: *Noturus furiosus* (also occurs on the Piedmont), *Elassoma zonatum, Lepomis marginatus.*

The Tar and Neuse upland faunas are enriched by three Roanoke species of somewhat restricted distribution, *Moxostoma cervinum, Nocomis raneyi* (Lachner and Jenkins, 1971a) and *Ambloplites cavifrons* (in part, Smith, 1968), and by more widespread forms that apparently had the Roanoke as their center of evolution or as one center of dispersal on the Atlantic slope (*Chrosomus oreas, Notropis albeolus, N. ardens, N. v. volucellus, Etheostoma n. nigrum, Percina crassa roanoka* and *Stizostedion v. vitreum*). All of these, except *N. albeolus,* terminate southward on the Atlantic slope in the Neuse. Additional southern terminations in the Neuse, which occur in the Roanoke and well to its north, are *Lampetra aepyptera, Notropis bifrenatus* (Jenkins and Zorach, 1970), *Etheostoma o. olmstedi* and *E. vitreum.* The latter four forms typically inhabit lower gradients on the central Atlantic slope than do the ten listed immediately above.

A basis for much of the close relationships (table 7) between the upland faunas of the Neuse-Tar and Roanoke was given above. The chief direction of upland divide transgression has probably been from the Roanoke to the

Neuse-Tar, as indicated by phyletic relationships of the Roanoke fauna (see below) and probable drainage history. The lower Roanoke River and Dan River of the Roanoke drainage lack large southern tributaries (fig. 1); it would appear that hypothetical streams of the Roanoke drainage were pirated by the Neuse and Tar, favoring enrichment of the captors with more species than gained by the Roanoke. Lachner and Jenkins (1971a) give additional evidence of connections among the Roanoke, Neuse and Tar drainages. These captures would have transpired on the Piedmont or Coastal Plain and would have transferred species mainly of these provinces. Evidence exists that the large majority of Roanoke forms that are absent from the Neuse and Tar are restricted to, or are most successful, in portions of the Roanoke draining the Blue Ridge and Ridge and Valley provinces. These forms are: *Salvelinus fontinalis, Campostoma anomalum michauxi, Exoglossum maxillingua, Notropis cerasinus, N. chiliticus, Rhinichthys a. atratulus, Hypentelium roanokense, Moxostoma ariommum, M. erythrurum, M. hamiltoni, M. rhothoecum, Noturus gilberti, Cottus b. bairdii, Etheostoma podostemone, Percina peltata* subsp. and *P. rex.* Of lowland Roanoke fishes, only *Lampetra lamottei,* the large stream inhabitant *Carpiodes cyprinus* and *Etheostoma olmstedi atromaculatum* are not known from the Neuse and Tar. Although some of these forms, such as *Salvelinus* and *Cottus,* would probably be prevented from forming populations in the Neuse and Tar because of absence or limitation of suitable habitat, most do occur in Piedmont portions of the Roanoke (although some are uncommon or rare therein).

A single record of *Catostomus c. commersonii* is known from the Neuse: South Flat River, on the Piedmont of Person County, North Carolina, at the Route 501 bridge about three miles south of Timberlake, taken in 1963 by R. D. Ross (collection 1579), R. L. Miles and Jenkins. This sucker is widespread in the upper Tar (Ratledge *et al.*, 1966; Menhinick *et al.,* ms.) and upper and middle Roanoke. *Etheostoma f. flabellare,* is another upland form that is rare in the Neuse and Tar.

ROANOKE FAUNA.—The Roanoke fauna is numerically the richest and most distinctive on the Atlantic slope of the United States. Among its 83 species and subspecies are 6 endemics; 2 are exclusively shared and 13 are slightly more widespread. At least the large majority of the characteristic Roanoke fishes (*i.e.,* apparently autochthonous or upper Teays basin derivatives) have their closest relationships with fishes extant in the New drainage or in the southwestern Ohio basin. Ross (1969) reviewed some of these relationships, but other studies indicate that some of his comments warrent clarification or modification. All characteristic Roanoke forms are members of the upland or upland-montane fauna of the upper Roanoke, within the Ridge and Valley and upper Piedmont provinces. Most are uncommon or rare in the more sandy-bottomed upper Chowan system, which drains the lower Piedmont. The distribution of many species in middle and lower Piedmont streams of the Roanoke proper is poorly known since few collections have been taken from these waters. In the following discussion, presence in the New drainage of the characteristic Roanoke forms or their close relatives is noted.

Among Roanoke cyprinids, *Nocomis raneyi* is most closely related and allopatric to *Nocomis platyrhynchus,* a New River drainage endemic that is primitive within the *Nocomis micropogon* species group (Lachner and Jenkins, 1971a). *Chrosomus oreas* is most closely related to an undescribed form recognized by Ross and Carico (1963:9, 12). *C. oreas* occurs in the New and on the central Atlantic slope; the undescribed form occurs very locally in Tennessee tributaries from the lower Clinch system down to approximately the Tennessee-northeastern Alabama State Line (Henshall, 1889, as *Chrosomus erythrogaster*), and probably to northwestern Alabama (Gilbert, 1891:147). The Roanoke and New have two syntopic species, *Notropis albeolus* and *Notropis cerasinus,* of the *Notropis cornutus* species group (subgenus *Luxilus*), whose heritage is to the Ohio basin and westward; *N. cerasinus* is primitive within its species group (Gilbert, 1964; Menzel, 1970). *Notropis procne* probably had its early history partly in the Roanoke, as indicated by the apparent confinement of its closest relative, *Notropis* sp., the paleband shiner, to the Tennessee and Cumberland drainages and by the Roanoke being in the center of its wide range on the Atlantic slope (Jenkins, ms.).

Catostomids account for the greatest proportional enrichment of the Roanoke fauna; it has nearly as many species of suckers (14 species, table 3) as the richest ones, the Tennessee and Cumberland faunas, each with 17. All Roanoke suckers, except two species of *Erimyzon,* occur commonly in the upper Roanoke, and at least 8, and possibly 11 species are present locally. Ecologically and morphologically, the Roanoke suckers constitute a highly diverse group. Ten of the Roanoke suckers, including all those of limited distribution, are in the tribe Moxostomatini. Of the two species of *Hypentelium* (Raney and Lachner, 1947), the Roanoke endemic, *H. roanokense,* possibly evolved more directly than *H. nigricans* from a widespread central and southern Appalachian stock (Jenkins, 1970). The subgenus *Thoburnia, sensu stricto,* the torrent or rustyside suckers, is a central Appalachian endemic group consisting of two closely related forms, *Moxstoma rhothoecum* and *M. hamiltoni.* The latter is a Roanoke endemic. The presence of *M. rhothoecum* in the Roanoke was noted by Ross (1969) and the writers; it also occurs in the New, James and Potomac drainages. The closest relationships of *Thoburnia, sensu stricto,* are probably with *Moxostoma* (*Scartomyzon*) *cervinum,* a Roanoke semi-endemic, and *Hypentelium* (Jenkins, 1970). The remarkable Roanoke endemic *Moxostoma* (*Scartomyzon*) *ariommum* is probably more intimitely related to the Green drainage relict *Moxostoma atripinne,* which was described and placed in *Thoburnia* (Bailey, 1959), than the latter is to *Thoburnia, sensu stricto.* (Jenkins, 1970). The present distribution of the *Scartomyzon—Thoburnia—Hypentelium* lineage includes notable disjunctions between the ranges of closely related species (Robins and Raney, 1956, 1957; Bailey, 1959), indicating that the eastern Teays basin was one of its major centers of distribution. Three of the four redhorse suckers, *Moxostoma* (*Moxostoma*) in the Roanoke and elsewhere on the central and south Atlantic slope are conspecific with widespread Mississippi basin species [*M. anisurum, M. erythrurum, M. macrolepidotum*] (Jenkins, 1970). The fourth, *M. pappillosum,* is a distinctive species ranging from the Roanoke south to the Santee. All four are absent from the New.

The madtom catfish, *Noturus gilberti,* exclusively shared with the James drainage, lacks an obvious close relative, but resembles in certain features the predominantly Mississippi basin species, *Noturus flavus,* of the monotypic subgenus *Noturus* (Taylor, 1969:108, 128, 220). We note that their coloration in life and habitat are similar. *N. gilberti* is regarded as a specialized relict of Teays basin ancestry. The form of *Noturus insignis* from the Roanoke and New river drainages was not recognized nomenclaturally by Taylor (1969: 90). The closest relative of this widespread Atlantic slope species appears to be *Noturus nocturnus* of the Mississippi basin and Gulf slope (Taylor, 1969:82, 89, 220).

Ambloplites cavifrons, the Roanoke rockbass, is notable among centrarchids in having a small range (the Roanoke, Neuse and Tar). It is a derivative of the widespread *Ambloplites rupestris,* which apparently is native to the New. Recognition of *A. cavifrons* as a subspecies (Fowler, 1945:41; Ross, 1969: 288) is not followed herein, nor is the report (Ross, 1969) from the James drainage accepted, for lack of substantiating data. As indicated by Raney (*in* Ross, 1969), rockbasses of the Roanoke drainage present an unsolved systematic problem. Although regarded as virtually extirpated from the Roanoke (Ross, 1969), typical specimens of *A. cavifrons* were recently taken from the Pigg River, a Roanoke tributary on the upper Piedmont. This species is being cultured for stocking purposes in North Carolina.

The endemic Roanoke logperch, *Percina rex,* is more closely related to the blotchside logperch, *Percina burtoni,* of the Tennessee and Cumberland drainages than to *Percina c. caprodes.* The former two species have a relict distribution and are probably more primitive than *P. c. caprodes* (Jenkins and T. Zorach, ms.). The affinities of the central Atlantic slope darter, *Percina crassa roanoka,* may be closer to *Percina evides* than to *Percina c. crassa.* It is doubtful that *roanoka* is a subspecies of *P. crassa. P. c. roanoka* is also known from the New; *P. evides* is a Mississippi basin species that is absent from the New. As in the Neuse-Tar drainage group, *Etheostoma nigrum* has differentiated in the Roanoke almost to the subspecific level; the Roanoke race was probably derived from the New drainage, where this species still occurs.

Two Roanoke endemics may have their closest affinity to Atlantic slope form. One is an undescribed subspecies of *Percina peltata* (Raney and Suttkus, 1948); the *peltata* species-group is found only on the Atlantic slope. However, this group is in the subgenus *Alvordius,* which has its greatest diversity, and probably its center of evolution, in the Mississippi basin. The Roanoke form may be a relict of a Mississippi stock; the *P. peltata* group attains its greatest diversity in the region of the Roanoke and adjacent drainages to the north and south. The endemic riverweed darter, *Etheostoma podostemone,* is most closely related to *Etheostoma longimanum,* an endemic of the James drainage. These are geminate species thought to be most closely related to the *Etheostoma olmstedi* complex of the Atlantic slope (Cole, 1957). They may, rather, represent a single stock of the subgenus *Boleosoma* derived from Mississippi basin ancestors (Cole, this volume). Gilbert (1961) and Miles (1964) also postulated that these species arose from the same parental stock.

Phyletic and geographic relationships of the endemic and other fishes characteristic of the upper Roanoke fauna indicate that the New drainage, and the Ohio (eastern Teays) basin in general, were the major contributors to this fauna. Preference of upland habitats by these Roanoke fishes lend credence to this hypothesis, by indicating that the fauna was not basically derived from Piedmont and Coastal Plain faunas of other drainages on the Atlantic slope. Additional evidence from probable stream history was given in the discussion of the Neuse-Tar fauna. Certain fishes appear to have originated in the Roanoke drainage, namely, *Nocomis raneyi* and *Ambloplites cavifrons* which have extant precursors in the New. Others of limited distribution, shared by the Roanoke and New or whose parental forms were probably extirpated from the New, could have arisen in either of these drainages. More widely distributed species and subspecies, or their basal stocks, that may have reached the central Atlantic slope from the New by crossing the upper Roanoke divide are *Salvelinus fontinalis, Campostoma anomalum michauxi* (Ross and Carico, 1963:11-12), *Clinostomus f. funduloides, Notropis analostanus* (Gibbs, 1963: 524), *N. ardens* (Ross, 1969: 289), *N. v. volucellus, Carpiodes cyprinus, Hypentelium nigricans, Moxostoma erythrurum* (Jenkins, 1970), *Ictalurus platycephalus* (Yerger and Relyea, 1968:381), *Cottus b. bairdii, Etheostoma flabellare brevispinna* (Ross, *in* Ross and Carico, 1963:13) and *Stizostedion v. vitreum.*

Ample opportunities for passage through the Roanoke-New (Teays) divide apparently existed. Geological evidence of captures is cited in the section on "Means of Dispersal". The importance of Roanoke-New captures is recognized by several ichthyologists, among whom are Ross (1952, 1969), Ross and Carico (1963), Robins and Raney (1956), Cole (1957), Gilbert (1964), Lachner and Jenkins (1971a) and Lachner and Wiley (1971). Cope (1868: 53) hinted at stream capture but did not then grasp its full significance. The

Roanoke apparently was the pirate in captures involving both the Roanoke proper and the Dan system of the Roanoke; these have a shorter course to the sea than the New, and the present upper New watershed is quite narrow (fig. 1). In addition to small-stream piracies, the Roanoke may have captured a major segment of the New, the hypothetical Fincastle River (Ross, 1969). Such a capture was implied by Ross (1969:285) to have predated smaller, detected captures. Diversion of Fincastle River would have permitted transfer to, and isolation in, the Roanoke of at least most of the upper Teays fauna. This is in harmony with the Roanoke being a major center of speciation and distribution on the Atlantic slope and with the hypothesis that a significant portion of its fauna comprises primitive or older members of species groups and subgenera. Absence from the Roanoke of several species of the New River drainage may relate to their entry into, or origination in, the New after the Fincastle River piracy.

The upper Roanoke was thought (White, 1953) to have formerly been part of a major drainage that included portions of the present upper Santee, Peedee, James, Rappahannock and Potomac drainages. Yerger and Relyea (1968:381) named the main channel of this drainage White's River, and stated that it provided a major dispersal route between the Roanoke, Peedee and Santee. However, if this river existed during early and middle Tertiary, it would probably have had little effect on present distribution of freshwater fishes. Differences among faunas of its supposed constituent drainages suggests an unlikelihood of a middle and late Quaternary existence. Dietrich (1959: 29, 32, 43-48) gave weighty evidence for disagreeing with some of White's basic assumptions and conclusions. Ross (*in* Yerger and Relyea, 1968) indicated that recent evidence "supports the former existence of White's River, but only as far north as the Roanoke River, which presumably was its outlet to the ocean."

A species most likely to have reached the Roanoke by a small-stream capture from the Peedee is *Notropis chiliticus,* exclusively shared by these drainages. It probably arose in the Peedee, where it is widespread, from a southern Appalachian stock of the subgenus *Hydrophlox* (Swift, 1970); it is limited in the Roanoke to the upper Dan system.

The Roanoke has only a moderately speciose lower Piedmont and Coastal Plain fauna, whose main distinction is the presence of several forms reaching their northern limits. Range termination of Coastal Plain forms roughly coincides with restriction of their typical habitat northward. Although an ample amount of this habitat actually seems to be present in certain tributaries of the western lower Chesapeake basin, for example the Chickahominy systems of the lower James drainage, such tributaries may have been barred by estuarine conditions in their lower setcions. Lower water temperatures northward may also have been a limiting factor.

The following are northern terminations: *Notropis alborus, N. altipinnis* (Hubbs and Raney, 1948), ***N. procne longiceps* (Raney, 1947), *,** *Moxostoma anisurum* (also occurs in St. Lawrence drainage), ***M. papillosum* (Jenkins, 1970), *Ictalurus platycephalus,* **Chologaster cornuta* (Woods and Inger, 1957), *Fundulus lineolatus* (Brown, 1958), *F. rathbuni, Pomoxis nigromaculatus,* **Micropterus s. salmoides* (Cope, 1870: 451), *Etheostoma collis lepidinion,* **Etheostoma serriferum* (Collette, 1962), and *Percina peltata nevisense.* Three typically upland species, *Notropis albeolus, N. chiliticus* and *Ambloplites cavifrons* also have their northern limits within this drainage.

Southern terminations are upland and lowland fishes: *Lampetra lamottei, Exoglossum maxillingua, Notropis cerasinus, Moxostoma erythrurum, M. rhothoecum, Noturus gilberti, Cottus b. bairdii* and *Etheostoma olmstedi atromaculatum.*

Several species most characteristic of the upper Roanoke fauna may soon be endangered by impoundments, pollution and introductions.

JAMES FAUNA.—The upland and montane fauna of the James comprises numerous fishes characteristic of the Chesapeake basin and is enriched by several species of Roanoke or Teays derivation. Its fairly depauperate lowland fauna is most similar to those northward. The James-Roanoke divide has been recognized (Raney, 1950; Miller, 1959; fig. 1; Gilbert, 1964) as forming one of the sharpest ichthyofaunal boundaries on the Atlantic slope, although recent studies found more Roanoke fishes in the James than known prior to Raney's (1950) analysis. The faunal break between the James and Roanoke is affected by, in addition to endemic forms, 17 range terminations (listed above) in the Roanoke, from southern drainages, and 9 terminations in the James, from the North, of upland or upland-montane fishes: *Nocomis micropogon* (Lachner and Jenkins, 1971a), *Notropis cornutus* (Gilbert, 1964), *N. p. procne* (Raney 1947), *N. r. rubellus, Rhinichthys cataractae,; Semotilus corporalis, Cottus cognatus* (Raney, 1950), *Percina n. notogramma* (Hogarth and Woolcott, 1966), *P. p. peltata* (Raney and Suttkus, 1948). The James-Roanoke break is sharpest with regard to catostomids; only 8 of 14 Roanoke species are known from the James. Fishes of the James that are most likely to have entered its upper portion from the Roanoke or New drainages or both are: *Campostoma anomalum michauxi, Chrosomus oreas, Nocomis raneyi, Notropis ardens, N. cerasinus, N. v. volucellus, Moxostoma erythrurum, Noturus gilberti, Percina c. roanoka, Stizostedion v. vitreum.*

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*—forms which actually terminate just north of the Roanoke, in the Dismal Swamp-Nansemond system, but were arbitrarily included as northern terminations in the Roanoke.

**—forms about as common in the upper Roanoke as in the lower.

Invasion of the James was probably via captures involving smaller streams of the surrounding Roanoke, New and drainages of the Chesapeake basin, and by utilization of the Greater Susquehanna River. Ross (1969) gave geological evidence that the James captured most of Fincastle River from the Roanoke subsequent to piracy of Fincastle River from the Teays by the Roanoke. Nearly the entire present portion of the upper James, northwest of the Blue Ridge (fig. 1), would have been part of Fincastle River, indicating a large stream capture. A biological contradiction to this hypothetical sequence of captures is that the faunas of the upper James and Roanoke are rather different. In addition, six of their shared species have a limited distribution in the James, suggesting that they entered the James relatively recently by a small stream connection(s) (in part, Lachner and Jenkins, 1971a). If at least most upper Roanoke fishes occupied Fincastle River prior to its capture by the James, then the upper James would be expected to have acquired most of them when it obtained Fincastle River. Since the upper James drainage does not appear to be faunally saturated and has abundant habitat similar to that in the upper Roanoke, we see little merit in postulating that some Roanoke fishes were competitively replaced in, or otherwise extirpated from the James.

Three endemic fishes occur in the James. *Notropis semperasper,* known only from the upper portion of the drainage, was thought (Gilbert, 1961) to be most closely related to *Notropis scepticus,* an Atlantic slope Piedmont species that terminates northward in the Cape Fear drainage. If these actually are so closely related, the gap between their ranges would be one of the longest and most peculiar on the Atlantic slope. Gilbert (1961) also suggested that *N. semperasper* has close affinities with *Notropis scabriceps,* an endemic of the New drainage. From the morphology of these fishes, we believe that the latter is probably the more plausible; these species may be geminate derivatives of common Teays stock. *Percina notogramma montuosa* was described (Hogarth and Woolcott, 1966) as the middle and upper James replacement of the nominate subspecies, which occurs in the lower James and extends north to the Patuxent drainage. The third endemic, *Etheostoma longimanum,* is the upper James geminate species of the Roanoke endemic *Etheostoma podostemone* (Cole, this volume; Miles, 1964). The James race of *Etheostoma n. nigrum* is distinctive but probably not sufficiently so to be named (Cole, this volume).

Forms having the northern end of their Atlantic slope range terminating in the James (discounting occurrence in the St. Lawrence drainage) are *Campostoma anomalum michauxi, Nocomis raneyi, Notropis ardens, N. v. volucellus, Moxostoma cervinum, M. erythrurum, Noturus gilberti, Lepomis gulosus, Percina crassa roanoka* and *Stizostedion v. vitreum.*

YORK AND RAPPAHANNOCK FAUNAS.—The York and Rappahannock are small drainages with fairly small faunas. Composition of their faunas reflects the encompassment of the York and Rappahannock by the James and Potomac drainages (table 7) and the fact that they were once tributary to the Greater Susquehanna River. They are isolated by divides and distance from the Roanoke and New faunas. *Chrosomus oreas* is the only element of the Teays fauna with a limited range occurring in the York. No such element is native to the Rappahannock. In comparison, the Neuse and Tar are also small drainages, but the diversity of their faunas was enhanced by adjacency to the Roanoke. Only one form, *Etheostoma olmstedi vexillare,* is exclusively shared by the York and Rappahannock; these drainages lack endemic forms and have low Distinction Indices (table 6).

Several species are not common to both drainages. This is possibly related to insufficent collecting, habitat differences, or inundation. Species apparently native to the Rappahannock, but not to the York, are *Salvelinus fontinalis, Ericymba buccata, Cottus b. bairdii* (Robins, 1954), *Etheostoma f, flabellare* and *Perca flavescens.* The first, third and fourth are typically upland or montane fishes on the central Atlantic slope and may have been limited in the York by lack or paucity of suitable habitat, as this drainage heads on the Piedmont — the Rappahannock begins in the Blue Ridge. *Ericymba* probably entered the Rappahannock from the Potomac; the only other drainage where it is known on the Atlantic slope is the more northern Susequehanna. Species and subspecies of York fishes not found in the Rappahannock are *Amia calva, Umbra pygmaea, Nocomis l. leptocephalus, Semotilus atromaculatus, Noturus gyrinus. Acantharcus pomotis, Centrarchus macropterus, Enneacanthus obesus, Lepomis gibbosus, Etheostoma nigrum* and *E. o. olmstedi.* All, except the speices of *Nocomis* and *Semotilus* and both species of *Etheostoma,* are, on the central Atlantic slope, more or less restricted to lowlands. All, except the speices of *Nocomis* and *Centrarchus,* occur in the Potomac and northward. Thus, their habitat, or access to it, may be limited in the Rappahannock. Possibly these forms dispersed along the Greater Susquehanna, through the lower Rappahannock, and found isolated areas of their habitat. If once established, however, their populations may have been extirpated with change to estuarine conditions during Holocene transgression of the sea (Oaks and Coch, 1963).

POTOMAC FAUNA.—The Potomac fauna is moderate in size (58 forms) and lacks endemic and exclusively shared forms. *Cottus girardi* was described as a Potomac endemic (Robins, 1961) but was synonymized (Savage, 1962) with *Cottus b. bairdii*. Relationships of the Potomac fauna are close to those of the western Chesapeake basin and the Susquehanna drainage fauna (composition partly from Greeley, 1936; and Carlson, 1968). The coastal fauna is fairly small; its size and composition is similar to, and probably determined largely by the same factors which affect(ed) that of the southwestern Chesapeake basin. *Moxostoma rhothoecum,* found in swiftwaters of the Shenandoah system (Miller, 1946; Raney and Lachner, 1946; Ross, 1959a), is the only species represented that is clearly assignable to the Roanoke-Teays fauna; another, *Chrosomus oreas,* is regarded as probably introduced. The former is the only species in more than one central Atlantic slope drainage with the northern end of its range in the Potomac. *Etheostoma vitreum* and *Percina n. notogramma* extend just north to the Patuxent drainage. Forms with the southern limit of their native Atlantic slope distribution in the Potomac are *Notropis s. spilopterus, Pimephales notatus, Semotilus m. margarita, Percopsis omiscomaycus* and *Percina c. semifasciata. Etheostoma b. blennioides* (Schwartz, 1965) and *Percina c. caprodes* are confined to the Potomac on the Atlantic slope. *Campostoma a. anomalum* is distributed similarly to these two, if all other stoneroller populations farther south are referrable to the subspecies *michauxi. Rhinichthys atratulus obtusus* has been recorded from the Potomac by Hubbs and Lagler (1958), but whether populations on the south Atlantic slope represent this subspecies remains to be resolved. Reports of *Notropis atherinoides,* another western fish, in the Potomac are based on *Notropis amoenus* (Snelson, 1968:795).

Although the Greater Susquehanna River was probably used by large stream fishes to enter and disperse from the Potomac, stream captures may have been more important agents for inter-drainage dispersal of many Potomac fishes. The occurrence of the Ohio basin fishes *Rhinichthys atratulus obtusus, Etheostoma b. blennioides* (Schwartz, 1965; Miller, 1968) and *Percina c. caprodes* only in the Potomac, of central Atlantic slope drainages, indicates their transferral by capture from the Monongahela drainage to the Potomac. The Potomac population of *Nocomis micropogon* bears evidence of introgressive hybridization, that apparently occurred in the Monongahela with *N. platyrhynchus* (Lacner and Jenkins, 1971a). Additional evidence of the importance of capture is the presence and distribution of fishes in the Potomac and Susquehanna drainage and their apparent absence from western Chesapeake drainages, with suitable habitat, between the Potomac and Susquehanna. Such circumstances point to the past existence of a direct lower Potomac-lower Susquehanna connection, evidence for which was given by Ross (1952:88). *Campostoma a. anomalum* and *Ericymba buccata* probably entered the Susquehanna directly from the Potomac, based on their wide distribution in the latter and confinement in the Susquehanna to its lower portion (in part, Ross, 1958b; Wallace, 1969). Many members of the Potomac upland fauna, although unidentified due to their wide distribution on the Atlantic slope, may also have used such a route. Two fishes, *Notropis s. spilopterus* (Gibbs, 1957b: 205) and *Semotilus m. margarita,* which have their southern limits on the Atlantic slope in the Potomac drainage, and which occur in the upper Monongahela drainage and the eastern Great Lakes basin, may have entered the Potomac from the Monongahela and the Susquehanna by a glacial outlet; both are unknown from other Chesapeake drainages. They possibly gained access to the Potomac from the Susquehanna, or vice versa, or crossed the divide in both directions. *S. m. margarita* is more likely to have done so as it is a small-stream inhabitant. The trout-perch, *Percopsis omiscomaycus,* and *Percina caprodes semifasciata* are northern forms occurring in the lower Susquehanna and terminating southward in the Potomac drainage. They obviously reached the Potomac from the north (Atlantic slope) as they are absent from the upper Monongahela. Whether they used a direct route to the Potomac from the Susquehanna, took the Greater Susquehanna, or both routes, is uncertain. Their inhabitation of large streams favors the Greater Susquehanna route. Indications that *Percina caprodes semifasciata* used at least the upper portion of the Susquehanna extension are records (Bailey and Gosline, 1955:36; Mansueti, 1964:37) from tributaries of northern Chesapeake Bay near the present Susquehanna mouth; these records may also represent populations recently established through a low-salinity bridge afforded by the Susquehanna.

MONONGAHELA FAUNA.—The Monongahela drainage is a major part of the upper Ohio basin. Its fauna of at least 80 species and subspecies lacks endemic and other species of highly restricted distribution. Two major stream systems, the Monongahela and the Youghiogheny, form the Monongahela drainage; they meet near the junction of the Monongahela and Allegheny Rivers, which forms the Ohio River. Fishes known from the Monongahela but not the Youghiogheny are *Hiodon tergisus, *Clinostomus f. funduloides, *Exoglossum laurae, Ericymba buccata, Hybopsis a. amblops, Notropis r. rubellus, Semotilus m. margarita, Percopsis omiscomaycus, Etheostoma b. blennioides,* and **Percina oxyrhyncha.* Absence of some of these from the Youghiogheny probably relates to pollution, insufficient collecting, or both. Others [indicated by an asterisk] probably reached the Monongahela from the New River drainage by stream capture as they have been found only in the upper Monongahela. In addition, the Monongahela population of *Nocomis micropogon* shows effects of apparent introgressive hybridization with *N. platyrhynchus,* which probably dispersed from the New into the Monongahela (Lachner and Jenkins, 1971a). Fishes at least once known in the Youghiogheny and unknown from the Monongahela are *Hybopsis d. dissimilis, Minytrema melanops, Moxostoma macrolepidotum breviceps, Pylodictis olivaris, Percina macrocephala* and *Stizostedion canadense;* these apparent distributional anomalies may also relate to to recent extirpation or insufficient collecting.

Several fishes reported from the Allegheny drainage (Raney, 1939), the other major drainage of the upper Ohio, are unknown from the Monongahela, probably a function of pollution or insufficient collecting, particularly in large streams and rivers. These are *Ichthyomyzon bdellium* (Lachner, ms.), *I. greeleyi, Lampetra lamottei, Acipenser fulvescens, Scaphirhynchus platorynchus, Polyodon spathula, Hybognathus n. nuchalis, Carpiodes c. carpio, Ictiobus bubalus, Cycleptus elongatus, Noturus eleutherus, Etheostoma m. maculatum, E. tippecanoe* and *Percina evides.* Additional species regarded as euryhaline or catadromous on the Atlantic and Gulf slopes could be added to this list. The apparent absence from the Monongahela of other Allegheny fishes is possibly related to lack of suitable habitat in the former or the fishes reached the Allegheny from the Lake Erie drainage by stream capture (see section on Effects of the Pleistocene), and since then, have had insufficient time to reach the Monongahela. These fishes are *Umbra limi, Esox americanus vermiculatus, E. lucius, Campostoma anomalum pullum, Chrosomus erythrogaster, Nocomis biguttatus, Notropis d. dorsalis, N. heterodon, N. heterolepis, N. umbratilus cyanocephalus* and *Culaea inconstans.*

South-Central Ohio Basin Fauna.—Drainages herein regarded as part of the south-central Ohio basin are, in sequence of entering the Ohio River beginning upriver, the Little Kanawha, Kanawha (excluding from this discussion its upper section, the New River drainage), Guyandot and Big Sandy. The faunas of these drainages are closely related. Their sizes range from small (44 forms in Guyandot) to moderately large (86 forms in Kanawha), although probably all species present have not been recorded (see section "Diversity by Drainage"). Endemic forms are absent. Only the Kanawha has an exclusively shared species; contributions by the New River fauna to this and other faunas are treated below.

Falls in the upper portion of the Little Kanawha appear to have had little influence on species distribution within this drainage. Small-stream fishes below but not above these falls are *Chrosomus erythrogaster, Etheostoma caeruleum* and *E. f. flabellare.* Forms both above and below the falls are *Campostoma a. anomalum, Nocomis micropogon, Notropis r. rubellus, Pimephales promelas, Semotilus atromaculatus, Catostomus c. commersonii, Moxostoma duquesnii, M. erythrurum, Noturus flavus, Cottus b. bairdii, Etheostoma n. nigrum* and *E. variatum. Etheostoma z. zonale* is the only form known above but not below the falls; it is probably present below.

Faunas of major drainages are progressively richer passing southwest of the Big Sandy. Increments in species are probably due partly to increasing proximity to the rich faunas of the Tennessee and Cumberland drainages and those of the Ozark region and the lower Mississippi Valley. Forms endemic to the Green or Kentucky drainages (fig. 1), or with a wider but limited distribution in the region of these drainages, are *Moxostoma atripinne* (Green drainage; Bailey, 1959), *Etheostoma bellum* (Green drainage; Zorach, 1968), *Etheostoma sagitta spilotum* (Kentucky drainage; Kuehne and Bailey, 1961), *Etheostoma* sp., a new species of barcheek darters of the subgenus *Catonotus* (Green drainage; Kuehne and Small, Jr., ms.), two undescribed forms of the subgenus *Ulocentra* of *Etheostoma* in the Green drainage (Winn, 1958), one in the Kentucky and Cumberland drainages (Kuehne and Bailey, 1961) and an undescribed form related to *Percina cymatotaenia* in the Green drainage and Red River system of the Kentucky drainage (in part, Bailey *in* Collette, 1965: 576).

TENNESSEE AND CUMBERLAND FAUNAS.—Rich faunas are harbored in the southwestern Ohio basin by the Tennessee and Cumberland drainages, excluding the portion above Cumberland Falls. The Tennessee has 191 species and subspecies, of which 27 are endemic and 19 exclusively shared; respective totals for the Cumberland are 150, 6 and 15. The two faunas are closely related (table 7) and exclusively share 13 forms (table 2). Their relationships are probably even closer (and faunas richer) since the following lowland or large-water species, known from the lower Tennessee but not reported from the lower Cumberland, probably occur in the latter: *Amia calva, Esox niger, Notropis fumeus, Elassoma zonatum, Elassoma* sp., *Lepomis marginatus, Etheostoma chlorosomum, E. histrio, E. proeliare, Percina shumardi* and *P. uranidea*. Similarly, *Notropis shumardi, Notropis volucellus wickliffi* and *Ammocrypta asprella,* known from the Cumberland, will probably be found in the Tennessee.

Several factors apparently relate to the richness of these faunas and to the greater number of total and endemic forms in the Tennessee than in the Cumberland. Close proximity to the large faunas of the Ozark upland region and lowlands of the lower Mississippi Valley enhanced the likelihood of faunal exchange. The Tennessee and Cumberland rivers enter the Ohio River a few miles apart and near the mouth of the Ohio; the Ohio joins the Mississippi close to the northeastern fringe of the Ozarks. During part of the Pleistocene, the Ohio, Tennessee and Cumberland apparently entered the Mississippi considerably below their present mouths, effecting more direct connection with the southern Ozarks. In addition to contributing large-river or turbid-river fishes to the Tennessee and Cumberland, the Mississippi and lower Ohio (and Teays) rivers probably acted as a filter bridge for fishes of eastern and western uplands, permitting limited trans-Mississippi dispersal and subsequent isolation and speciation. Aspects of drainage history and trans-Mississippi fish distribution and evolution are discussed by Pflieger (1969), Gibbs (1961), Miller (1968) and Lachner and Jenkins (1971a, b). In an earlier section (Stream Capture), we argue on geological grounds that the Tennessee fauna is composed of predominantly autochthonous and other Mississippi basin elements and imply that peripheral faunas on the Atlantic and Gulf slopes may have contributed relatively little to the Tennessee. These have, however, provided some enrichment for the Tennessee. Additions to the Tennessee fauna from the rich Mobile drainage are discussed by Smith-Vaniz (1968) and Ramsey (ms.). The Cumberland fauna is not adjacent to those of the Atlantic and Gulf slopes; thus, it has probably been less enriched by members of these faunas than has the Tennessee. On the other hand, elements of more northern faunas of the Ohio basin occur in the Cumberland and not in the Tennessee.

The large area of the Tennessee and Cumberland drainages favors, at least indirectly, development and support of rich faunas therein. The Tennessee drainage is between two and three times the size of the Cumberland, a factor which might have differentially affected the richness of their faunas. Larger drainage size would offer greater opportunity for isolation of stocks by distance, such as in springs or montane systems separated by inter-connecting rivers of different habitat. A more fundamental factor is the diversity of habitat afforded within hydrographic boundaries (discussed above). The Tennessee has the most diverse, or nearly the most diverse, habitats among drainages in the region, comprising, in addition to upland streams, moderate numbers of lowland streams and considerable montane ones. Both drainages include springs or spring-like streams in their lower sections; these are more abundant in the Tennessee.

Pleistocene glacial periods probably had a significant part in effecting the distinct differences in size and composition between the Tennessee-Cumberland fauna and those of other drainages of the southern and the northern Ohio basin. The differences may relate partly to glacial advances and cool climates that forced fishes southward into refugia, with disruption or retardation of speciation of formerly isolated stocks. The more southerly located Tennessee-Cumberland fauna would likely have been less affected by such factors, the Tennessee even less than the Cumberland.

Enrichment of the Tennessee and Cumberland faunas probably transpired reciprocally, through exchange of fishes by dispersal between the mouths of these streams and stream captures. It seems more proper to equate patterns of present distribution with captures that probably occurred during Quaternary time (some described by Ross, ms.), rather than with a hypothetical history of the Tennessee and Cumberland drainages (summarized by Adams, 1915), the main events of which are thought to have occurred in the early and mid-Tertiary.

Categorization of Tennessee drainage fishes according to sections and general habitat that they occupy reveals interesting aspects of the distribution of the endemic and exclusively shared fauna. The three faunal categories are the upper Tennessee, *i.e.,* upriver from and including the Chickamauga River system (the first major eastern tributary system below the montane region, fig. 1), the lower Tennessee, below the Chickamauga, and both areas. Although knowledge of the distribution of the fishes within the Tennessee is incomplete, it is unlikely that the range of many forms will be significantly extended with more data. Total forms in each category are 35 in the upper Tennessee, 55 in the lower Tennessee and 101 in both sections.

Of the 35 forms in the upper Tennessee only, 18 are endemic, constituting 67 per cent of the 27 Tennessee endemics. The 18 are *Ichthyomyzon hubbsi, Chrosomus oreas* subsp., *Hybopsis cahni, H. insignis eristigma, Notropis s. spectrunculus, N. spectrunculus* subsp., *Phenacobius crassilabrum, Noturus baileyi, N. flavipinnis, Cottus baileyi, Etheostoma acuticeps, E. blennioides gutselli, E. maculatum vulneratum, E. swannanoa,* two undescribed species of *Etheostoma,* the dusttail and greenfin darters, *Percina aurantiaca* and *P. evides* subsp. Six are exclusively shared forms, *Clinostomus funduloides* subsp., *Notropis rubricroceus, Notropis* sp., the paleband shiner, *Cottus bairdii* subsp., *Percina burtoni* and *P. squamata.* Three are southeastern or slightly more widespread forms (*Campostoma anomalum michauxi, Cottus* sp. and *Etheostoma flabellare brevispinna*). Eight are widespread in the Ohio basin or elsewhere, namely, *Salvelinus fontinalis, Rhinichthys, cataractae, Ammocrypta pellucida* (Woolman, 1892), *Etheostoma camurum, Etheostoma f. flabellare, Etheostoma tippecanoe* (Zorach, 1969), *Percina copelandi* and *P. macrocephala* (Ramsey and Williams, ms.). The occurrence of many of the above forms only in the upper portion of the Tennessee correlates with the considerable extent of montane habitat in the eastern portion of the upper Tennessee. Of these 35 forms, 12 typically occur in montane streams, 11 in montane and upland areas, 11 in uplands and 1 in uplands and lowlands. Although a high proportion of the Tennessee endemics and other fishes with small ranges are restricted to or occur in montane waters, the montane fauna is distinctly less speciose than the upland fauna.

Confinement, or nearly so, of several endemics mainly to the montane region and the presence of their closest relatives in upland portions of systems originating in the montane or adjacent regions of the Tennessee are notable aspects of distribution within this drainage. The montane fishes and their nearest relatives, shown in parentheses, are *Hybopsis insignis eristigma* (*H. i. insignis*), *Notropis s. spectrunculus* and *N. spectrunculus* subsp. (*Notropis* sp., the sawfin shiner, Ramsey, ms.), *Phenacobius crassilabrum* (possibly *P. uranops,* Minckley and Craddock, 1962), *Cottus baileyi* and *Cottus* sp. (undetermined member(s) of *C. bairdii* species-group, Robins, 1961), *Etheostoma blennioides gutselli* (*E. b. newmanii,* Miller, 1968), *Etheostoma* sp., the greenfin darter (*E. camurum,* Zorach, ms.) and *Percina evides* subsp. (*P. e. evides,* Denoncourt. 1969). Members of most of these pairs occur sympatrically or are represented by intergrades in one or more streams in fringes of the montane region. None of the above pairs have subspecies on the adjacent portion of the Atlantic slope; apparently only *Percina evides* and the two *Cottus* are represented there by specifically distinct close relatives. Stocks of the montane forms may have entered the Tennessee and differentiated, followed by ingress to the Tennessee of their relatives. Differentiation may instead have been by the second form of each pair to enter the Tennessee, implying that the montane form may be the more primitive of the two. Ancestral populations of montane forms may not have been preadapted to montane conditions; the forms of each pair may have been ecologically incompatible upon meeting in the Tennessee, resulting in one adapting more to montane conditions and the other to uplands. As most of the montane forms are only subspecifically distinct from their relatives, it is likely that they adapted to the highlands at least partly during times of isolation rather than genetic interchange.

Other montane or montane-upland fishes endemic to the Tennessee, or confined to south and central eastern United States, including the Tennessee, are *Ichthyomyzon hubbsi* (Raney, 1952), *Campostoma anomalum michauxi, Chrosomus oreas* subsp., *Clinostomus funduloides* subsp. (Deubler, 1955), *Notropis coccogenis* (Gilbert, 1964), *N. leuciodus* and *N. rubricroceus* (Swift, 1970), *Rhinichthys atratulus obtusus, Etheostoma acuticeps, E. flabellare brevispinna, E. maculatum vulneratum* (Zorach and Raney, 1967), *E. rufilineatum* (Zorach, ms.), *E. swannanoa* (Richards, 1966), *Percina aurantiaca* and *P. squamata*. Some of these fishes are allopatric to close relatives that also occur in the Tennessee. Others represent groups or species-pairs probably originally or long-adapted to the southern and central Appalachians; the history of some involves Atlantic slope drainages.

NEW AND UPPER CUMBERLAND FAUNAS.—Both drainages have a downstream waterfall each constituting a natural barrier, ranking among the largest on main rivers east of the Rocky Mountains (fig. 1). The drop at Kanawha Falls, separating the New-Kanawha watershed into its two components, is about 24 feet in natural height. Construction of a dam at the falls in 1898 has raised the New River elevation by 3 feet (E. J. Boyle, Manager, Union Carbide Corporation plant, Alloy, West Virginia, pers. comm.). Cumberland Falls is about 85 feet high (Wilson and Clark, 1914: 5, Pl. 1; Stansbery, 1969; cover of recent Fisheries Bulletins, Kentucky Department of Fish and Wildlife Resources).

Faunas above the falls differ sharply in number of species from those below and from most adjacent faunas. (Distinct ichthyofaunal differences also occur between faunas of the upper Mississippi basin above and below St. Anthony Falls, Minnesota [Eddy *et al.,* 1963].) The New drainage fauna includes 47 forms, whereas 86 occur below the falls, in the Kanawha drainage, and in the adjacent Roanoke and Tennessee drainages there are 83 and 191 forms, respectively. There are 38 forms above Cumberland Falls, while the middle and lower Cumberland contains a total of 150. The fauna of the upper Kentucky drainage is not as rich as that of the entire Cumberland, but it has distinctly more species than that of the upper Cumberland. The New drainage fauna probably was richer in pre-Holocene times and more similar, than now, to faunas presumed to have occurred in the upper and middle Teays and the early southwestern Ohio basins. Evidence for this is the occurrence in the Roanoke of several forms related to species and subspeices of the Tennessee and their absence from the geographically intermediate New (see Roanoke Fauna). The disjunct forms probably were once represented in the New by populations that have been extirpated. The upper Cumberland may also have been a major route of faunal exchange (Lachner and Jenkins, 1971a). It is unlikely that these disjunct or relict patterns of distribution resulted from dispersal of stocks between the Ohio basin and central Atlantic slope by a route south of the Appalachians (for example, routes on the Gulf slope discussed in relation to lowland, spring and cave fishes by Woods and Inger, 1957: 250, 255; Collette and Yerger, 1962: 220, 228-229; Crossman, 1966: fig. 5; and Yerger and Relyea, 1968: 379-380).

A combination of several factors seemingly effected the depauperate nature of the New and upper Cumberland faunas. Among these are prevailing ecological conditions, such as high gradient, hard bottom and poorly developed flood plains (in the New: Addair, 1944; Ross and Perkins, 1959; upper Cumberland: Woodlman, 1892; Wilson and Clark, 1914). A high dissolved sulfate content has been suggested as a factor in the New (Ross and Perkins, 1959). Although worthy of further study, sulfates may not have been sufficiently widespread to significantly limit the richness of the New fauna; high concentrations, apparently, are local and greatly diluted by the New River (Ross and Perkins, 1959). There apepars to be fairly wide variation in rock types and water chemistry in the New of Virginia (Shoup, 1948; Ross and Perkins, 1959). permitting development of a somewhat speciose fauna. The range in chemical characters of upper Cumberland streams appears to be smaller than that below Cumberland Falls and above Kanawha Falls; the streams are underlaid with sandstones and shales (Charles, 1966; Carter and Jones, 1969), and may be only of low productivity. The New fauna may have been reduced by loss of surface flow to subterranean drainage and extensive dismemberment of tributaries by stream captures (Ross and Perkins, 1959: 10). Pollution from coal mines and other sources have sharply reduced aquatic life in portions of the New and upper Cumberland within historic times.

Small size of the faunas above Kanawha and Cumberland falls relates to absence or paucity of lowland habitat, reflected by high Average Gradient Indices of these faunas (table 9). It is noted that, in this respect, the differences between faunas above and below falls may not be fully expressed by considering the total size of each fauna. High gradient and scarcity of soft bottoms, in general, in the New correlate with the apparently native occurrence therein of only three centrarchids and three catostomids. Two of the latter, *Catostomus c. commersonii* and *Hypentelium nigricans,* are widespread in the New and elsewhere and common in montane habitats. The other sucker, *Moxostoma rhothoecum,* is rare and locally distributed in the New; reasons for this are not apparent, as its preferred habitat — riffles in small streams, both warm and cool ones — is abundant in the New. The depauperacy of catostomids is striking in respect to the wealthy sucker faunas of the upper Tennessee and Roanoke drainages. Soft-bottom dwellers found in the New, but only in its lower section where they are uncommon or rare, are *Ericymba buccata, Notropis s. stramineus* and *Etheostoma n. nigrum. Hybopsis d. dissimilis* also is apparently confined in the New to its lower section, but its habitat is common in much of the New. While small size of the New fauna may be partly attributable to a limited amount of low gradient areas, it should be noted that parts of New River and some of its larger tributaries are characterized by frequent long pools. Some do have a considerable amount of soft bottom (Ross and Perknis, 1959; our observations), although in many cases, this may have resulted from recent excavation, deforestation and consequent erosion in their valleys rather than from more natural processes.

Other fishes have a curious distribution in the New that does not seem to relate closely to gradient. *Nocomis l. leptocephalus, Notropis ardens, N. cerasinus* and *Noturus insignis* are widespread in the Virginia portion of the New, but are apparently absent from its tributaries arising in North Carolina and West Virignia (Lachner and Jenkins, 1971a). *Chrosomus oreas* and *Notropis albeolus* have similar distributions, but extend downstream into the upper portion of the section in West Virginia (into the Greenbriar River system). *Exoglossum maxillingua, Notropis galacturus* and *Percina c. roanoka* are known only from a small part of the New in Virginia (Ross and Carico, 1963; Jenkins, ms.). These small ranges may have resulted from these fishes having first entered the New during recent time, or re-entered after extirpation. Ross and Perkins (1959) suggested that *N. albeolus* and *N. ardens* are distributed in the New according to a preference for softwater streams. Two closely related darters, *Etheostoma kanawhae* and *E. osburni,* approximate and replace each other in the middle New; the former occurs widely in the upper section, the latter in the lower. Certain cottids may have restricted distributions in the New; study of recent collections is needed to verify this.

Pleistocene glacial periods probably influenced reduction of the New (Ross and Perkins, 1959: 10) and upper Cumberland faunas. Parts of the upper Cumberland drainage arise at elevations of about 3500 feet, and in the New at somewhat greater heights; the average elevation of these drainage basins is considerably lower and elevations at the falls are not particualrly high (Kanawha Falls, about 650 feet; Cumberland Falls, about 850 feet). Montane portions of other drainages in the study region arise at heights similar to those in many New and upper Cumberland tributaries. Although much remains to be learned of Pleistocene climate in these drainages, it is known that temperatures were cooler during glacial peroids than at present (Hack, 1969: 6, 16). Cooler climates would tend to force warm water fishes into lower elevations of the New and upper Cumberland, to below their falls, and perhaps lower their reproductive potential, resulting in their extinction. The most speciose family in the New, in proportion to total forms in each family of the region, is the cool-adapted Cottidae: three of seven forms are present. In cases of extirpation from the New and upper Cumberland during the Pleistocene, the height of the falls in these streams probably barred re-entry from downstream. Reaccess to upper sections from lower elevations within other central Appalachian drainages seems to have been present, at least by main river channels. Ross and Perkins (1959) stated that the possible past occurrence of small montane glaciers in the Appalachians should not be overlooked, and cited evidence of such conditions. In addition, Stose (1922: 24) gave evidence of glacial action in the Potomac drainage. Glacial effects would be additive to those caused by colder climates. However, Hack and Goodlett (1960) showed that features suggesting periglacial activity can originate under present climatic conditions.

Five endemics are included in the New fauna, constituting a higher percentage of endemicity (10 per cent) than in all other central Appalachian faunas except the Tennessee (table 4). The endemics are *Nocomis platyrhynchus* (Lachner and Jenkins, 1971a), *Notropis scabriceps, Phenacobius teretulus* (Minckley and Craddock, 1962), *Cottus carolinae* subsp. (Robins, 1954) and *Etheostoma kanawhae* (Raney, 1941a). *N. platyrhynchus* probably entered the Monongahela drainage and hybridized with *Nocomis micropogon*; the former is not now found in the Monongahela. A supposed endemic, *Notropis kanawha,* was shown to be an interspecific hybrid (Bailey and Gilbert, 1960). *Etheostoma osburni,* long regarded as an endemic, is shared with the Kanawha drainage, where it is known only from the Elk River system; it may have entered the Elk River via capture with the Gauley River system of the lower New (fig. 1). Two other species once thought to be confined to the New, or nearly so, have much wider ranges. *Exoglossum laurae* occurs as relict populations in southwestern Ohio (Trautman, 1957) and the Monongahela drainage (Jenkins, ms.), and it is widespread in the Allegheny drainage and Genesee system (Lake Ontario drainage) above its falls (Raney, 1941b); it is not known from the Kanawha drainage. *Percina oxyrhyncha* inhabits the Monongahela and extends down the Kanawha in certain of its tributaries, possibly intergrading with a close relative, *Percina phoxocephala,* in eastern Kentucky.

Fishes found in tributaries of the lower New River and not in the Kanawha may be retarded from downstream movement and passage over Kanawha Falls by the more rigorous habitats of rapids, cascades and low falls in the extensive gorge of lower New River. Gradient and other physical features in the lower New were described by Reger (1926) and illustrated by Campbell and Mendenhall (1896); a longitudinal profile of the entire New River, showing increased gardient in its lower section, was given by Hack (1969: fig. 3).

The upper Cumberland fauna lacks endemic species and has contributed its apparently few autochthonous fishes to the middle Cumberland. *Etheostoma kennicotti* is the only upper Cumberland species unreported below Cumberland Falls; it occurs elsewhere in southern Illinois, the Green drainage and, widely, in the Tennessee drainage. *Etheostoma s. sagitta* (regarded as an endemic in tables herein) was recently found in the South Fork system, a major tributary of the middle Cumberland near, but below, the falls (Carter and Jones, 1969: 35). A geminate subspecies, *E. sagitta spilotum,* inhabits the upper Kentucky drainage (Kuehne and Bailey, 1961). *Etheostoma* (*Ulocentra*) sp., the emerald darter, is restricted to the upper Kentucky and upper Cumberland drainages and, in the middle Cumberland, to systems from the South Fork upstream (Kuehne and Bailey, 1961: 7; Carter and Jones, 1969: 43, 49). The emerald darter may have entered the middle Cumberland from the Kentucky by stream piracy (fig. 1). The upper Cumberland population of *Etheostoma nigrum* was recognized as an endemic subspecies, *susanae,* by Kuehne and Bailey (1961: 7). We do not recognize this form and note that *E. nigrum* was reported from the middle Cumberland by Carter and Jones (1969: 23, 38).

Zoogeographic Aspects of Certain Aquatic Invertebrates

Many of the dominant patterns of distribution, diversity and endemism found in central eastern fishes are paralleled by freshwater mussels, snails and crayfishes. Although much knowledge of these groups remains to be gained and summarized, the following works permit general comments: on mussels, Ortmann (1913, 1925), Wilson and Clark (1914), van der Schalie (1939), van der Schalie and van der Schalie (1950); on pleurocerid snails, Ortmann (1913); on crayfishes, Ortmann (1913), Hobbs (1969).

The Mississippi basin contains the richest of these invertebrate faunas. The Cumberlandian faunas, including those of the Tennessee and Cumberland drainages, are quite varied and are marked by numerous endemic forms. More northern drainages of the Ohio basin have fewer speices and endemics, of none, than the Cumberland. The faunas above the falls in the New and upper Cumberland are depauperate; the New fauna shows relationships with that of the upper Tennessee. Central Atlantic slope faunas are not as rich as most faunas of the Ohio basin, and contain elements of the latter and autochthonous ones. A faunal break occurs in the northern sector of the central Atlantic slope; the James may be included with the Roanoke in the southern group and the Potomac in the more northern fauna. A striking departure from the usual pattern of fish distribution is that the upper Roanoke faunas are apparently depauperate.

SUMMARY

Composition, origin, distribution and dispersal of the freshwater fish faunas of central Appalachian drainages, including their sections in Piedmont, Plateau and Coastal Plain areas, are treated. Major drainages studied of the central Atlantic slope (east of the Atlantic-Mississippi or Ohio basin divide) extend from the Peedee north to the Potomac. Those west of the divide are part of the Ohio River basin: the Tennessee and Cumberland drainages of the south western Ohio; the Big Sandy, Guyandot, New-Kanawha and Little Kanawha drainages of the south-central Ohio; the Monongahela drainage of the upper Ohio. The New drainage is that portion of the New-Kanawha above Kanawha Falls; the upper Cumberland is separated from the middle Cumberland by Cumberland Falls: both waterfalls are major barriers. Fishes are tabulated by drainages, stream gradients and the sizes of stream that they inhabit; introduced and certain euryhaline or diadromous fishes are included.

The native freshwater fish fauna of the area comprises about 277 species or, at least, 313 species and subspecies (forms) distributed among 22 families. Fifty-one (16 per cent) of the 313 or endemics (occur in a single drainage) and 31 (10 per cent)are excluisevly shared (occur in only two drainages). The most speciose families are ostariophysans-minnows (Cyprinidae), suckers (Catostomidae), catfishes (Ictaluridae) and perciforms—sunfishes and basses (Centrarchidae) and darters (Percidae); these include 271 (87 per cent) of the 313 forms. Upland faunas generally have more species and more endemic forms than lowland and montane fauna. This relationship is partly associated with abundance and stability o fhabitats in the area.

The Atlantic-Ohio divide is the most important boundary in the area. The Ohio basin contains more families (20) than the central Atlantic slope (16) and has 179 forms (57 per cent of the 313 treated) that are absent from the central Atlantic slope, compared with 77 (25 per cent) of the latter area that are not found in the Ohio basin; only 57 (18 per cent) forms occur on both sides of the divide. Thirty-nine (76 per cent) of the 51 endemics and 22 (71 per cent) of 31 exclusively shared forms occur only in the Ohio basin, Indices of Faunal Resemblance also reveal that relationships of individual drainage faunas of the Atlantic slope are almost always closer to those of other Atlantic slope drainages than to faunas of drainages of the Ohio basin.

The pattern of numerical diversity of drainage faunas on the central Atlantic slope does not show a close correlation with latitude, but northerly drain-

ages do tend to have smaller faunas. The most speciose Atlantic slope fauna is that of the Roanoke drainage (83 forms). Faunas south of the Roanoke, to the Peedee, tend to be richer (60 to 72 forms) than those north of the Roanoke to the Potomac (41 to 67 forms). The Roanoke has the highest number of endemics (6) on the central Atlantic slope. Drainage Distinction Indices indicate that the Roanoke has the most unique fauna on the Atlantic slope of the United States. Faunas south of the Roanoke tend to have higher Distinction Indices than those north of the Roanoke.

The Peedee fauna is closely related to adjacent faunas, the Santee on the South and the Cape Fear to the North. One of the most obvious faunal breaks on the Atlantic slope occurs between the Cape Fear and Neuse drainages. The Neuse and Tar faunas are intimately related; both are enriched by several fishes acquired from the distinctive Roanoke fauna. Despite numerous contributions by the Roanoke to the James fauna, the difference between them is sharp. Faunas from the James to the Potomac are fairly similar, sharing numerous fishes characteristic of the Chesapeake basin and more northern and western drainages.

Faunas of the Ohio basin tend to be richer than those on the Atlantic slope, the most speciose and distinctive being the Tennessee (191 forms, 27 endemics) and Cumberland (150 forms, 6 endemics). Numbers of forms in 4 south-central Ohio faunas range from 47 to 86; endemics are absent. The Monongahela fauna contains 80 forms and lacks endemics. Somewhat depauperate faunas occur in drainages above major waterfalls, particularly in the New (47 forms, compared with 86 below in the Kanawha) and upper Cumberland (38 forms, opposed to 150 total for the middle and lower Cumberland); the New has 5 endemics, the upper Cumberland none.

Numerical diversity of faunas is associated with diversity of habitat and abundance of each type of habitat within drainages. These factors are correlated with numbers of physiographic and/or biotic provinces drained and size of drainages. Historical factors also contribute to diversity. Enrichment of faunas apparently was by dispersal of species through presently conjoined river drainages (of the Ohio basin) and by dispersal through temporary connections between drainages, such as those effected by stream capture, and by extended rivers on the Atlantic slope during Pleistocene periods of lowered sea level. Closure of such routes provided opportunity for isolation and differentiation. The Roanoke, in particular on the Atlantic slope, apparently was a major center of evolution and dispersal of fishes derived from the Ohio basin by stream capture with the New drainage. Enlargement of faunas was enhanced by proximity to rich faunas; for example, by exchange of species among the Tennessee, Cumberland and other drainages of the central Mississippi basin. Small size of the New and upper Cumberland faunas probably relates to the presence of waterfalls acting as barriers and to the general absence of lowland habitat; cooler climate during glacial periods of the Pleistocene may have influenced extirpation of species from these faunas.

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ADDENDUM

Since this symposium, two manuscripts have been published that involve the names of species referred to in this paper. Our reference to *Notropis* sp. (F. F. Snelson, Jr., pers. comm.) under the Cape Fear fauna and Table 1 concerns *Notropis mekistocholas* Snelson (*1971, Copeia, No. 3*: 449-462). *Etheostoma* sp. (Kuehne and Small, Jr., ms.), a barcheek darter, subgenus *Catonotus*, endemic to the Green River drainage, was named *Etheostoma barbouri* Kuehne and Small (*1971. Copeia, No. 1*: *18-26*). The study referred to in the text and Literature Cited, Pflieger, W. L. (*1969. Dissertation Abstracts, 30*[*6*]: *2 p.*) was published (*1971. A distributional study of Missouri fishes.—Publications, University of Kansas, Museum of Natural History. 20*[*3*] *:225-570, 15 figs., 193 maps*). Cavender, Lundberg, and Wilson (*1970. Two new fossil records of the genus* Esox [*Teleostei, Salmoniformes*] *in North America.—Northwest Science, 44*[3] *:176-183*) provided a summary, based on fossil and Recent fishes, of similarities and differences between faunas east and west of the Continental Divide.

LITERATURE CITED

ADAMS, C. C. 1915. The variations and ecological distribution of the snails of the genus *Io*.—Memoirs, National Academy of Science, 12 (Part 2), 94 pp.

ADDAIR, J. 1944. The fishes of the Kanawha River system in West Virginia and some factors which influence their distribution.—Doctoral Dissertation, Ohio State University, Columbus, Ohio, 225 pp.

BAILEY, R. M. 1938. A systematic revision of the centrarchid fishes, with a discussion of their distribution, variations, and probable interrelationships.—Doctoral Dissertation, University of Michigan, Ann Arbor, Michigan, 256 pp.

.... 1945. Review of: Some considerations on the distribution of fishes in Ontario, by I. Radforth.—Copeia (2): 125-126.

.... 1959. A new catostomid fish, *Moxostoma* (*Thoburnia*) *atripinne*, from the Green River drainage, Kentucky and Tennessee.—Occasional Papers, Museum Zoology, University of Michigan, Number 599, 19 pp.

.... and M. O. ALLUM. 1962. Fishes of South Dakota.—Miscellaneous Publications, Museum of Zoology, University of Michigan, Number 119, 131 pp.

BAILEY, R. M. and C. E. BOND. 1963. Four new species of freshwater sculpins, genus *Cottus*, from western North America.—Occasional Papers, Museum of Zoology, University of Michigan, Number 634, 27 pp.

BAILEY R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, and W. B. SCOTT. 1970. A list of common and scientific names of fishes from the United States and Canada. 3rd ed.—American Fisheries Society, Special Publication, No. 6, 149 pp.

BAILEY, R. M. and C. R. GILBERT. 1960. The American cyprinid fish *Notropis kanawha* identified as an interspecific hybrid.—Copeia (4): 354-357.

BAILEY, R. M. and W. A. GOSLINE. 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae.—Miscellaneous Publication, Museum of Zoology, University of Michigan, Number 93, 44 pp.

BAILEY R. M., H. E. WINN, and C. L. SMITH. 1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes.—Proceedings, Academy of Natural Sciences, Philadelphia, 105: 109-164.

BERG, C. O. 1963. Middle Atlantic States, p. 191-237. *In* Frey, David G. (Ed.), Limnology in North America.—University of Wisconsin Press, Madison, Wisconsin.

BROWN, J. L. 1955. Local variation and relationships of the cyprinodont fish *Fundulus rathbuni* Jordan and Meek.—Journal, Elisha Mitchell Scientific Society, 71(2): 207-213.

.... 1958. Geographic variation in southeastern populations of the cyprinodont fish *Fundulus notti* (Agassiz).—American Midland Naturalist, 59(2): 477-488.

CAMPBELL, M. R. 1896. Drainage modifications and their interpretation.—Journal of Geology, 4(5): 567-581, 657-678.

.... and W. C. MENDENHALL. 1896. Geologic section along New and Kanawha rivers in West Virginia.—Seventeenth Annual Report, United States Geological Survey (for 1895-1896), Part 2: 479-511.

CARLSON, F. T. 1968. Report on the biological finding, p. 5-41. *In* Suitability of the Susquehanna River for restoration of shad.—United States Department of the Interior, Bureau of Commercial Fisheries.

CARTER, J. P. and A. R. JONES. 1969. Inventory and classification of streams in the upper Cumberland River drainage of Kentucky.—Fisheries Bulletin, Number 52, Department of Fish and Wildlife Resources, Frankfort, Kentucky, 70 pp.

CHARLES, J. R. 1966. Effects of coal-washer wastes on biological productivity in Martin's Fork of the upper Cumberland River.—Fisheries Bulletin, Number 27-B, Department of Fish and Wildlife Resources, Frankfort, Kentucky, 39 pp.

CLAY, W. M. 1962a. A field manual of Kentucky fishes.—Kentucky Department of Fish and Wildlife Resources, Frankfort, Kentucky, 147 pp.

.... (ed.) 1962b. Aquatic-life resources of the Ohio River.—Ohio River Valley Water and Sanitation Commission, Cincinnati, Ohio, 218 pp.

CLEARY, R. E. 1956. The distribution of the fishes of Iowa, p. 267-324. *In* J. R. Harlan and E. B. Speaker, Iowa fish and fishing, 3rd Edition.—State Conservation Commission, Des Moines, Iowa.

COLE, C. F. 1957. The taxonomy of the percid fishes of the genus *Etheostoma*, subgenus *Boleosoma*, of eastern United States.—Doctoral Dissertation, Cornell Universtiy, Ithaca, New York, 395 pp.

.... 1958. The taxonomy of the percid fishes of the genus *Etheostoma*, subgenus *Boleosoma*, of eastern United States.—Dissertation Abstracts, 18(3): 1155-1156.

.... 1967. A study of the eastern Johnny darter, *Etheostoma olmstedi* Storer (Teleostei, Percidae).—Chesapeake Science, 8(1): 28-51.

COLLETTE, B. B. 1962. The swamp darters of the subgenus *Hololepis* (Pisces, Percidae).—Tulane Studies in Zoology, 9(4): 115-211.

.... 1965. Systematic significance of breeding tubercles in fishes of the family Percidae.—Proceedings, United States National Museum, 117(3518): 567-614.

.... and R. W. Yerger. 1962. The American percid fishes of the subgenus *Villora*.—Tulane Studies in Zoology, 9(4): 213-230.

COPE, E. D. 1868. On the distribution of fresh-water fish in the Allegheny region of southwestern Virginia.—Journal, Academy of Natural Sciences, Philadelphia, (Series 2) 6(5): 207-247.

.... 1869. Synopsis of the Cyprinidae of Pennsylvania.—Transactions, American Philosophical Society, 13 (New series) Part 3: 351-410.

.... 1870. A partial synopsis of the fishes of the fresh waters of North Carolina.—Proceedings, American Philosophical Society, 11: 448-495.

CROSSMAN, E. J. 1966. A taxonomic study of *Esox americanus* and its subspecies in eastern North America.—Copeia (1): 1-20.

CURRAY, J. R. 1965. Late Quaternary history, continental shelves of the United States, pp. 723-735. *In* H. E. Wright, Jr. and David G. Frey (eds.), The Quaternary of the United States.—Princeton University Press, Princeton, New Jersey.

DAGET, J. 1968. Diversite des faunes de poissons dans les cours d'eau du Portugal. —Arquivos, Museu Bocage, Lisbon, Portugal, vol. 2, Notes e Suplementos, number 15: 21-26.

DARLINGTON, P. J., JR. 1957. Zoogeography: The geographical distribution of animals.—John Wiley and Sons, New York, New York, 675 pp.

DARTON, N. H. 1894. Outline of Cenozoic history of a portion of the middle Atlantic slope.—Journal of Geology, 2(6): 568-587.

DENDY, J. S. 1946. Further studies of depth distribution of fish, Norris Reservoir, Tennessee.—Journal, Tennessee Academy of Science, 21(1): 94-104.

DENONCOURT, R. F. 1969. A systematic study of the gilt darter *Percina evides* (Jordan and Copeland) (Pisces, Percidae).—Doctoral Dissertation, Cornell University, Ithaca, New York, 216 pp.

DE SYLVA, D. P., F. A. KALBER, JR. and C. N. SHUSTER, JR. 1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on the species collected in deeper water.—University of Delaware Marine Laboratory, Information Service Publiaction Number 5, 164 pp.

DEUBLER, E. E. 1955. A taxonomic study of the cyprinid fish *Clinostomus vandoisulus* (Valenciennes) in the eastern United States.—Doctoral Dissertation, Cornell University, Ithaca, New York.

DIETRICH, R. V. 1959. Geology and mineral resources of Floyd County of the Blue Ridge upland, southern Virginia.—Bulletin, Engineering Experimental Station, Virginia Polytechnic Institute and State University, Series 134, 52(12):160 pp.

EDDY, S., J. B. MOYLE, and J. C. UNDERHILL. 1963. The fish fauna of the Mississippi River above St. Anthony Falls as related to the effectiveness ot this falls as a migration barrier.—Proceedings, Minnesota Academy of Science, 30(2): 111-115.

EMERY, K. O., R. L. WIGLEY, and M. RUBIN. 1966. A submerged peat deposit off the Atlantic coast of the United States.—Limnology and Oceanography, Special Supplement, Number 10: R97-R102.

EVERMANN, B. W. 1918. The fishes of Kentucky and Tennessee: a distributional catalogue of the known species.—Bulletin, United States Bureau of Fisheries, 35 (1915-16): 295-368.

.... and C. H. BOLLMAN. 1886. Notes on a collection of fishes from the Monongahela River.—Annals, New York Academy of Science, 3: 335-340.

EVERMANN, B. W. and U. O. COX. 1896. The fishe so fthe Neuse River basin.—Bulletin, United States Fish Commission for 1895:303-310.

EVERMANN, B. W. and S. F. HILDEBRAND. 1916. Notes on the fishes of east Tennessee.—Bulletin, United States Bureau of Fisheries, 34: 431-451.

FITZ, R. B. 1968. Fish habitat and population changes resulting from impoundment of Clinch River by Melton Hill Dam.—Journal, Tennessee Academy of Science, 43(1): 7-15.

FLEMER, D. A. and W .S. WOOLCOTT. 1966. Food habits and distribution of the fishes of Tuckahoe Creek, Virginia, with special emphasis on the bluegill, *Lepomis m. macrochirus* Rafinesque.—Chesapeake Science, 7(2): 75-89.

FORBES, S. A. and R. E. RICHARDSON. 1920. The fishes of Illinois. 2nd ed.—Illinois Natural History Survey, 3, 357 pp. (separate atlas).

FOWLER, H. W. 1945. A study of the fishes of the southern Piedmont and Coastal Plain.—Academy of Natural Sciences, Philadelphia, Monograph 7, 408 pp.

.... 1947. Description of a new species and genus of darter from the Cape Fear River basin of North Carolina.—Notulae Naturae of Academy of Natural Sciences, Philadelphia, Number 191, 3 pp.

FRANKEL, L. and H. F. THOMAS. 1966. Evidence of freshwater lake deposits in Block Island Sound.—Journal of Geology, 74: 240-240.

FREY, D. G. 1951. The fishes of North Carolina's Bay lakes and their intraspecific variation.—Journal, Elisha Mitchell Scientific Society, 67(1): 1-44.

FRIDLEY, H. M. 1933. Drainage diversions of the Cheat River.—Proceedings, West Virginia Academy of Science, 6: 85-88.

GERKING, S. D. 1945. The distribution of the fishes of Indiana.—Investigations, Indiana Lakes and Streams, 3(1): 1-137.

.... 1963. Central States, pp. 239-268. *In* Frey, David G. (ed.), Limnology in North Carolina.—University of Wisconsin Press, Madison, Wisconsin.

GIBBS, R. H., JR. 1957a. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. I. Systematic status of the subgenus *Cyprinella,* with a key to the species exclusive of the *lutrensis-ornatus* comples.—Copeia (3): 185-195.

——— 1957b. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. II. Distribution and variation of *Notropis spilopterus*, with the description of a new subspecies.—Lloydia, 20(3): 186-211.

——— 1961. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. IV. The *Notropis galacturus-camurus* complex.—American Midland Naturalist, 66(2): 337-354.

——— 1963. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. The *Notropis whipplei-analostanus-chloristius* complex.—Copeia (3): 511-528.

GILBERT, C. H. 1891. Report of explorations made in Alabama during 1889, with notes on the fishes of the Tennessee, Alabama, and Escambia Rivers.—Bulletin, United States Fish Commission, 9 (1889): 143-159.

GILBERT, C. R. 1961. *Notropis semperasper*, a new cyprinid fish from the upper James River system, Virginia.—Copeia (4): 450-456.

——— 1964. The American cyprinid fishes of the subgenus *Luxilus* (genus *Notropis*).—Bulletin, Florida State Museum, 8(2): 95-194.

GOLDSBOROUGH, E. L. and H. W. CLARK. 1908. Fishes of West Virginia.—Bulletin, United States Bureau of Fisheries, 27(1907): 29-39.

GREELEY, J. R. 1936. Fishes of the area with annotated list, pp. 45-88, *In* A biological survey of the Delaware and Susquehanna watersheds.—Supplement, 25th Annual Report (1935), New York State Conservation Department.

GREENE, C. W. 1935. The distribution of Wisconsin fishes.—Wisconsin Conservation Commisison, Madison, Wisconsin: 235 pp.

GREENWOOD, P. H. 1964. Explosive speciation in African Lakes.—Proceedings, Royal Institute Great Britain, 40, Number 184: 256-269.

GUNTER, G. 1956. A revised list of euryhalin fishes of North and Middle America. —American Midland Naturalist, 56(2): 345-354.

HACK, J. T. 1969. The area, its geology: Cenozoic development of the southern Appalachians, p. 1-17. *In* P. C. Holt (ed.), The distributional history of the biota of the southern Appalachians. Part I: Invertebrates.—Research Division Monograph 1, Virginia Polytechnic Institute and State University, Blacksburg, Va.

——— and J. C. GOODLETT. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians.—Professional Papers, United States Geological Survey, 347, 66 p.

HENSHALL, J. A. 1889. On a collection of fishes from east Tennessee.—Journal, Cincinnati Society of Natural History, 11(1): 31-33.

HILDEBRAND, S. F. and W. C. SCHROEDER. 1928. Fishes of Chesapeake Bay.—Bulletin, United States Bureau of Fisheries, 42(1): 1-366.

HOBBS, H. H., JR. 1969. On the distribution and phylogeny of the crayfish genus *Cambarus*, p. 93-178. *In* P. C. Holt (ed.), The distributional history of the biota of the southern Appalachians. Part I: Invertebrates.—Research Division Monograph 1, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

HOGARTH, W. T. and W. S. WOOLCOTT. 1966. The mountain stripeback darter, *Percina notogramma montuosa*, n. ssp. from upper James River, Virginia.—Chesapeake Science, 7(2): 101-109.

HOUGH, J. L. 1963. The prehistoric Great Lakes of North America.—American Scientist, 51(1): 84-109.

HOWDEN, H. F. and R. MANSUETI. 1951. Fishes of the tributaries of the Anacostia River, Maryland.—Proceedings, Biological Society of Washington, 64: 93-96.

HUBBS, C. L. 1941. The relation of hydrological conditions to speciation in fishes, pp. 182-195. *In* A symposium on hydrobiology.—University of Wisconsin Press, Madison, Wisconsin.

.... and K. F. LAGLER. 1958. Fishes of the Great Lakes Region.—Bulletin, Cranbrook Institute of Science, 26, 213 pp.

HUBB, C L. and R. R. MILLER. 1948. Correlation between fish distribution and hydrographic history in the desert basins of western United States, pp. 17-166. *In* The Great Basin, with emphasis on glacial and postglacial times.—Bulletin, University of Utah, Salt Lake City, Utah, 38 (20).

HUBBS, C. L. and E. C. RANEY. 1946. Endemic fish fauna of Lake Waccamaw, North Carolina.—Miscellaneous Publications, Museum of Zoology, University of Michigan, Number 65, 30 pp.

.... 1947. *Notropis alborus,* a new cyprinid fish from North Carolina and Virginia.—Occasional Papers, Museum of Zoology, University of Michigan, Number 498, 17 pp.

.... 1948. Subspecies of *Notropis altipinnis,* a cyprinid fish of the eastern United States.—Occasional Papers, Museum of Zoology, University of Michigan, Number 506, 20 pp.

HUBBS, CLARK. 1957. Distributional patterns of Texas fresh-water fishes.—Southwestern Naturalist, 2(2-3): 89-104.

JANSSEN, R. E. 1953. The Teays River, ancient precursor of the East.—Scientific Monthly, 77: 306-314.

JENKINS, R. E. 1970. Systematic studies of the catostomid fish tribe Moxostomatini. —Doctoral Dissertation, Cornell University, Ithaca, New York, 818 pp.

.... and T. ZORACH. 1970. Zoogeography and characters of the American cyprinid fish *Notropis bifrenatus.*—Chesapeake Science, 11(3): 174-182.

JORDAN, D. S. 1889. Report of explorations made during the summer and autumn of 1888, in the Allegheny region of Virginia, North Carolina and Tennessee, and in western Indiana, with an account of the fishes found in each of the river basins of those regions.—Bulletin, United States Fish Commission, 8(1888): 97-173.

.... 1928. The distribution of fresh-water fishes.—Smithsonian Institution Report for 1927. pp. 355-385.

.... and A. B. BRAYTON. 1878. Contributions to North American ichthyology. Based primarily on the collections of the United States National Museum. III. A. On the distribution of the fishes of the Allegheny region of South Carolina, Georgia, and Tennessee, with descriptions of new and little known species.—Bulletin, United States National Museum, 12: 7-95.

JORDAN, D. S. and J. SWAIN. 1884. List of fishes collected in the Clear Fork of the Girard (Pisces, Cyprinidae) of eastern United States, with descriptions of new species.—Smithsonian Contributions to Zoology, Number 85, 97 pp.

KEUP, L. and J. BAYLESS. 1964. Fish distribution at varying salinities in Neuse River basin, North Carolina.—Chesapeake Science, 5(3): 119-123.

KIRKWOOD, J. B. 1957. A brief study of the Levisa Fork and Russell Fork of the Big Sandy River.—Fisheries Bulletin, Number 21, Department of Fish and Wildlife Resources, Frankfort, Kentucky, 15 pp.

KIRSCH, P. H. 1892. Notes on the streams and fishes of Clinton County, Kentucky, with a description of a new darter.—Bulletin, United States Fish Commission, 10 (1890): 289-292.

.... 1893. Notes on a collection of fishes from the southern tributaries of the Cumberland River in Kentucky and Tennessee.—Bulletin, United States Fish Commission, 11(1891): 259-268.

KRUMHOLZ, L. A. 1958. Ohio River Valley Water Sanitation Commission—University of Louisville—Life Resources Project.—Second Annual Report, 1 July 1957—30 June 1958 and Quarterly Report Number 5, 1 April 1958—30 June 1958, Cincinnati, Ohio and Louisville, Kentucky, 128 pp.

.... and W. L. MINCKLEY. 1964. Changes in the fish population in the upper Ohio River following temporary pollution abatement.—Transactions, American Fisheries Society, 93(1) :1-5.

KUEHNE, R. A. and R. M. BAILEY. 1961. Stream capture and the distribution of the percid fish *Etheostoma sagitta*, with geologic and taxonomic considerations.—Copeia (1): 1-8.

KUHNE, E. R. 1939. A guide to the fishes of Tennessee and the mid-South.—Tennessee Department of Conservation, Nashville, 124 pp.

LACHNER, E. A. and R. E. JENKINS. 1967. Systematics, distribution and evolution of the club genus *Nocomis* (Cyprinidae) in the southwestern Ohio River basin with the description of a new species.—Copeia (3): 557-580.

.... 1971a. Systematics, distribution and evolution of the club genus *Nocomis* Girard (Pisces, Cyprinidae) of eastern United States with descriptions of new species.—Smithsonian Contributions to Zoology, Number 85, 97 pp.

.... 1971b. Systematics, distribution, and evoltuion of the *Nocomis biguttatus* species group (Family Cyprinidae: Pisces) with a description of a new species from the Ozark uplands.—Smithsonian Contributions to Zoology, Number 91 (in press).

LACHNER, E. A., C. R. ROBINS, and W. R. COURTENAY, JR. Exotic fishes and other aquatic organisms introduced into North America.—Smithsonian Contributions to Zoology, Number 59: 29 pp.

LACHNER, E. A. and M. L. WILEY. 1971. Populations of the polytpic species *Nocomis leptocephalus* (Girard) with a description of a new subspecies.—Smithsonian Contributions to Zoology, Number 92 (in press).

LENNON, R. E. 1962. An annotated list of the fishes of Great Smoky Mountains National Park.—Journal, Tennessee Academy of Science, 37(1): 5-7.

LINDSEY, C. C. 1956. Distribution and taxonomy of fishes in the Mackenzie drainage of British Columbia.—Journal, Fisheries Research Board of Canada, 13(6): 759-789.

LIVINGSTONE, D. A. 1953. The fresh water fishes of Nova Scotia.—Proceedings, Nova Scotian Institute of Science, 23(1), 90 pp.

LONG, C. A. 1963. Mathematical formulas expressing faunal resemblance.—Transactions, Kansas Academy of Science, 66(1): 138-140.

MACKIN, J. H. 1933. The evolution of the Hudson-Delaware-Susquehanna drainage. —American Journal of Science, 26: 319-331.

MANSUETI, R. J. 1964. Eggs, larvae, and young of the white perch, *Roccus americanus*, with comments on its ecology in the estuary.—Chesapeake Science, 5(1-2): 3-45.

MASSMANN, W. H. 1954. Checklist of the fishes of Virginia waters of Chesapeake Bay and its tidal tributaries.—Virginia Fisheries Laboratory, Gloucester Point, Virginia, 14 pp.

...................., E. C. LADD, and H. N. MCCUTCHEON. 1952. A biological survey of the Rappahannock River, Virginia.—Special Scientific Report, Number 6, Virginia Fisheries Laboratory, Gloucester Point, Virginia, 173 pp.

MCCABE, B. C. 1943. An analysis of the distribution of fishes in the streams of western Massachusetts.—Copeia (2): 85-89.

MENZEL, B. W. 1970. An electrophoretic analysis of the blood proteins of fishes of the subgenus *Luxilus* (*Notropis*: Cyprinidae).—Doctoral Dissertation, Cornell University, Ithaca, New York.

METCALF, A. L. 1966. Fishes of the Kansas River system in relation to zoogeography of the Great Plains.—Publications, Museum of Natural History, University of Kansas, 17(3): 23-189.

MILES, R. L. 1964. A systematic study of *Etheostoma longimanum* and *Etheostoma podostemone* (Pisces, Percidae).—Master of Science Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 129 pp.

MILLER, L. F. 1944. A comparison of the hoop-net catches in several fish habitats of Wheeler Reservoir.—Transactions, American Fisheries Society, (1943): 37-40.

MILLER, R. R. 1946. Distributional records for North American fishes, with nomenclatorial notes on the genus *Psenes*.—Journal, Washington Academ yof Sciences 36, (6): 206-212.

.... 1959. Origin and affinities of the freshwater fish fauna of western North America, p. 187-222. *In* Hubbs, C. L. (ed.) Zoogeography.—Publication Number 51, American Association for the Advancement of Science.

.... 1961. Speciation rates in some fresh-water fishes of western North America, p. 537-560. *In* W. F. Blair (ed.). Vertebrate speciation.—University of Texas Press, Austin, Texas.

.... 1965. Quaternary freshwater fishes of North America, p. 569-581. *In* H. E. Wright, Jr. and D. G. Frey (eds.). The Quaternary of the United States. —Princeton University Press, Princeton, New Jersey.

.... 1966. Geographical distribution of central American freshwater fishes. —Copeia (4): 773-802.

MILLER, R. V. 1968. A systematic study of the greenside darter, *Etheostoma blennioides* Rafinesque (Pisces: Percidae).—Copeia (1): 1-40.

MINCKLEY, W. L. and J. E. CRADDOCK. 1962. A new species of *Phenacobius* (Cyprinidae) from the upper Tennessee River system.—Copeia (2): 369-377.

MOORE, G. A. 1950. The cutaneous sense organs of barbeled minnows adapted to life in the muddy waters of the Great Plains region.—Transactions, American Microscopical Society, 69(1): 69-95.

MYERS, G. S. 1938. Fresh-water fishes and West Indian zoogeography.—Smithsonian Report for 1937, Publication 3465: 339-364.

.... 1949. Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems.—Bijdragen Tot De Dierkunde, 28: 315-322.

.... 1960. The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories.—Evolution, 14: 323-333.

.... 1966. Derivation of the freshwater fish fauna of Central America.—Copeia (4): 766-773.

OAKS, R. Q., JR. and N. K. COCH. 1963. Pleistocene sea levels, southeastern Virginia. —Science, 140: 979-983.

ORTMANN, A. E. 1913. The Alleghenian divide, and its influence upon the freshwater fauna.—Proceedings, American Philosophical Society, 52 (210): 287-390.

.... 1925. The naiad-fauna of the Tennessee River system below Walden Gorge.—American Midland Naturalist, 9(8): 321-371.

PATRICK, R. 1961. A study of the numbers and kinds of species found in rivers in eastern United States.—Proceedings, Academy of Natural Sciences, Philadelphia, 113(10): 215-258.

PFLIEGER, W. L. 1969. A distributional study of the fishes of Missouri.—Dissertation Abstracts, 30(6), 2 pp.

RADFORTH, I. 1944. Some considerations on the distribution of fishes in Ontario.—Contributions, Royal Ontario Museum of Zoology, Number 25, 116 pp.

RAMSEY, J. S. 1965. Zoogeographic studies on the freshwater fish fauna of rivers draining the southern Appalachian region.—Doctoral Dissertation, Tulane University, New Orleans, Louisiana, 130 pp.

RANDALL, J. F. 1958. The distribution of the fishes of the Catawba-Wateree River drainage basin, North Carolina and South Carolina.—Dissertation Abstracts, 18(1): 341-342.

RANEY, E. C. 1939. The distribution of the fishes of the Ohio drainage basin of western Pennsylvania.—Abstracts of Theses (1938), Cornell University, Ithaca, New York: 273-277.

——— 1941a. *Poecilichthys kanawhae,* a new darter from the upper New River system in North Carolina and Virginia.—Occasional Papers, Museum of Zoology, University of Michigan, Number 434, 16 pp.

——— 1941b. Range extensions and remarks on the distribution of *Parexoglossum laurae* Hubbs.—Copeia (4): 272.

——— 1947. Subspecies and breeding behavior of the cyprinid fish *Notropis procne* (Cope).—Copeia (2): 103-109.

——— 1950. Freshwater fishes, pp. 151-194. *In* The James River basin, past, present and future.—Virginia Academy of Science, Richmond, Virginia.

——— 1952. A new lamprey, *Ichthyomyzon hubbsi,* from the upper Tennessee River system.—Copeia (2): 93-99.

——— and E. A. LACHNER. 1946. *Thoburnia hamiltoni,* a new sucker from the upper Roanoke River system in Virginia.—Copeia (4): 218-226.

——— 1947. *Hypentelium roanokense,* a new catostomid fish from the Roanoke River in Virginia.—Novitates, Number 1333, American Museum of Natural History, 15 pp.

RANEY. E C. and W. H. MASSMANN. 1953. The fishes of the tidewater section of the Pamunkey River, Virginia.—Journal, Washington Academy of Science, 43(12): 424-432.

RANEY, E. C. and R. D. SUTTKUS. 1948. The subspecies of the shielded darter, *Hadropterus peltatus.*—Abstracts, Twenty-eighth Annual Meeting, American Society of Ichthyologists and Herpetologists, 1 p.

RATLEDGE, H. M., W. C. CARNES, and E. D. COLLINS. 1966. Checklist of fishes collected from the lotic waters of North Carolina 1960-1964.—Wildlife Resources Commission, Raleigh, North Carolina, 14 pp.

REGER, D. B. 1926. Mercer, Monroe, and Summers counties.—West Virginia Geological Survey, 963 pp.

RICHARDS, W. J. 1963. Systematic studies of darters from southeastern United States (Pisces, Percidae).—Doctoral Dissertation, Cornell University, Ithaca, New York, 203 pp.

——— 1966. Systematics of the percid fishes of the *Etheostoma thalassinum* species-group with comments on the subgenus *Etheostoma.*—Copeia (4): 823-838.

ROBINS, C. R. 1954. A taxonomic revision of the *Cottus bairdi* and *Cottus carolinae* species groups in eastern North America (Pisces, Cottidae).—Doctoral Dissertation, Cornell University, Ithaca, New York, 272 pp.

——— 1961. Two new cottid fishes from the fresh waters of eastern United States.—Copeia (3): 305-315.

.... and R. R. MILLER. 1957. Classifiaction, variation, and distribution of the sculpins, genus *Cottus,* inhabiting Pacific slope waters in California and southern Oregon, with a key to the species.—California Fish and Game, 43(3): 213-233.

.... and E. C. RANEY. 1956. Studies of the catostomid fishes of the genus *Moxostoma,* with descriptions of two new species.—Memoirs, Number 343, Cornell University Agricultural Experiment Station, 56 pp.

.... 1957. The systematic status of the suckers of the genus *Moxostoma* from Texas, New Mexico and Mexico.—Tulane Studies in Zoology, 5(12): 291-318.

ROSS, R. D. 1952. The subspecies and races of the cyprinid fish *Campostoma anomalum* (Rafinesque) in eastern United States.—Doctoral Dissertation, Cornell University, Ithaca, New York, 223 pp.

.... 1958a. Races of the cyprinid fish *Campostoma anomalum pullum* (Agassiz) in eastern United States.—Technical Bulletin, Virginia Agricultural Experiment Station, Number 136, 20 pp.

.... 1958b. Some taxonomic problems of Shenandoah River fishes.—Technical Bulletin, Virginia Agricultural Experiment Station, Number 137, 10 pp.

.... 1959a. Game fish streams and records of fishes from the Potomac-Shenandoah River system of Virginia.—Technical Bulletin, Virginia Agricultural Experiment Station, Number 140, 20 pp.

.... 1959b. Drainage evolution and distribution problems of the fishes of the New (upper Kanawha) River system in Virginia. Part 4. Key to the identification of fishes.—Technical Bulletin, Virginia Agricultural Experiment Station, Number 146, 27 pp.

.... 1969. Drainage evolution and fish distribtuion problems in the southern Appalachians of Virginia, pp. 277-292. *In* P. C. Holt (ed.), The distributional history of the biota of the southern Appalachians. Part I: Invertebrates.—Research Division Monograph 1, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

.... and J. E. CARICO. 1963. Records and distribution problems of fishes of the North, Middle, and South Forks of the Holston River, Virginia.—Technical Bulletin, Virginia Agricultural Experiment Station, Number 161, 23 pp.

ROSS, R. D. and B. D. PERKINS. 1959. Drainage evolution and distribution problems of the fishes of the New (upper Kanawha) River system in Virginia. Part 3. Records of fishes of the New River.—Technical Bulletin, Virginia Agricultural Experiment Station, Number 145, 35 pp.

ROSTLUND, E. 1952. Freshwater fish and fishing in native North America.—Publications in Geography, University of California, 9: 1-314.

ROTH, J. C. and S. E. NEFF. 1964. Studies of physical limnology and profundal bottom fauna, Mountain Lake, Virginia.—Technical Bulletin, Virginia Agricultural Experiment Station, Number 169, 44 pp.

ROUNSEFELL, G. A. 1958. Anadromy in North American Salmonidae.—Fishery Bulletin, United States Fish and Wildlife Service, 58(131): 171-185.

SAUER, C. O. 1927. Geography of the Pennyroyal.—Kentucky Geological Survey, 25 (Series 6): 5-303.

SAVAGE T. 1962. *Cottus girardi* Robins, a synonym of *Cottus bairdi* Girard.—Copeia (4): 848-850.

SCHUMM, S. A. 1965. Quaternary Paleohydrology, pp. 783-794. *In* H. E. Wright, Jr. and D. G. Frey (eds.). The Quaternary of the United States.—Princeton University Press, Princeton, New Jersey.

SCHWARTZ, F. J. 1963. Fresh-water minnows of Maryland.—Maryland Conservationist, 40(2): 19-29.

.... 1964. Natural salinity tolerances of some freshwater fishes.—Underwater Naturalist, 2(2): 13-15.

.... 1965. The distribution and probable postglacial dispersal of the percid fish, *Etheostoma b. blennioides,* in the Potomac River.—Copeia (3): 285-290.

SHATTUCK, G. B. 1906. The Pliocene and Pleistocene deposits of Maryland, pp. 23-137. —*In* Maryland Geological Survey, Pliocene and Pleistocene.

SHELDON, A. L. 1968. Species diversity and longitudinal succession in stream fishes. —Ecology, 49(2): 193-197.

SHOUP, C. S. 1948. Limnological observations on some streams of the New River watershed in the vicinty of Mountain Lake, Virginia.—Journal, Elisha Mitchell Scientific Society, 64(1): 1-12.

.... and S. H. PEYTON. 1940. Collections from the drainage of the Big South Fork of the Cumberland River in Tennessee.—Report, Reelfoot Lake Biological Station, 4: 106-116.

...................., and G. GENTRY. 1941. A limited biological survey of the Obey River and adjacent streams in Tennessee.—Report, Reelfoot Lake Biological Station, 5: 48-76.

SISK, M. E. 1969. The fishes of west Kentucky. I. Fishes of Clark's River.—Transactions, Kentucky Academy of Science, 30(3-4): 54-59.

SMITH, H. M. 1893. Report on a collection of fishes from the Albemarle region of North Carolina.—Bulletin, United States Fish Commission, 11: 185-200.

.... 1907. The fishes of North Carolina.—North Carolina Geological and Economic Survey, 2, 453 pp.

SMITH, P. W. 1965. A preliminary list of the lampreys and fishes of Illinois.—Biological Notes, Illinois Natural History Survey, Number 54, 12 pp.

SMITH, W. B. 1968. Roanoke bass, *Ambloplites cavifrons* Cope.—Progressive Fish Culturist, 30(3): 180.

SMITH-VANIZ, W. F. 1968. Freshwater fishes of Alabama.—Auburn University Agricultural Experiment Station, Auburn, Alabama, 211 pp.

SNELSON, F. F., JR. 1968. Systematics of the cyprinid fish *Notropis amoenus,* with comments on the subgenus *Notropis.*—Copeia (4): 776-802.

STANSBERY, D. H. 1969. Changes in the naiad fauna of the Cumberland River at Cumberland Falls in eastern Kentucky.—Annual Reports, for 1969, American Malacological Union (35th Annual Meeting), Bulletin Number 36: 16-17.

STEARNS, F. 1969. Bathymetric maps and geomorphology of the middle Atlantic Continental Shelf.—Fishery Bulletin, United States Fish and Wildlife Service, 68(1): 37-66.

STOSE, G. W. 1922. Geography, pp. 5-24. *In* G. W. Stose and H. D. Miser, Manganese deposits of western Virginia.—Bulletin, Virginia Geological Survey, Number 23.

SUTTKUS R. D. 1963. Order Lepisostei, pp. 61-88. *In* Fishes of the western North Atlantic.—Sears Foundation for Marine Research, Memoir Number 1, Part 3. Yale University, New Haven, Connecticut.

SWIFT, C. C. 1970. A review of the eastern North American cyprinid fishes of the *Notropis texanus* species group (subgenus *Alburnops*), with a definition of the subgenus *Hydrophlox,* and materials for a revision of the subgenus.—Doctoral Dissertation, Florida State University, Tallahassee, Florida.

TAYLOR, W. R. 1969. A revision of the catfish genus *Noturus* Rafinesque with an analysis of higher groups in the Ictaluridae.—Bulletin, United States National Museum, Number 282, 315 pp.

THOMPSON, H. D. 1939. Drainage evolution in the southern Appalachians.—Bulletin, Geological Society of America, 50(8): 1323-1356.

TRAUTMAN, M. B. 1957. The fishes of Ohio.—Ohio State University Press, Columbus, 683 pp.

TURNER, W. R. 1959. Pre-impoundment surveys of six Kentucky streams.—Fisheries Bulletin, Department of Fish and Wildlife Resources, Number 24, Frankfort, Kentucky, 43 pp.

.... 1961. Pre- and Post-impoundment surveys.—Report, Kentucky Department of Fish and Wildlife Resources, Project Number F-16-R-2, Frankfort, 75 pp.

UHLER, P. R. and O. LUGGER. 1876. List of the fishes of Maryland.—Report, Commissioners of Fisheries of Maryland, Annapolis: 81-208.

UNDERHILL, J. C. 1957. The distribution of Minnesota minnows and darters in relation to Pleistocene glaciation.—Occasional Papers, Minnesota Museum of Natural History, Number 7, 45 pp.

UYENO. T. and R. R. MILLER. 1963. Summary of late Cenozoic freshwater fish records for North America.—Occasional Papers, Museum of Zoology, University of Michigan, Number 631, 34 pp.

VAN DER SCHALIE, H. 1939. Additional notes on the naiades (fresh-water mussels) of the lower Tennessee River.—American Midland Naturalist, 2(2): 452-457.

.... and A. VAN DER SCHALIE. 1950. The mussels of the Mississippi River.—American Midland Naturalist, 44(2): 448-466.

WALLACE, D. C. 1969. A study of the ecology and life history of the silverjaw minnow, *Ericymba buccata* Cope (Pisces, Cyprinidae).—Doctoral Dissertation, Cornell University, Ithaca, New York, 196 pp.

WATSON, T. L. and J. H. CLINE. 1913. Drainage changes in the Shenandoah Valley region of Virginia.—Bulleti, Scientific Series, Philosophical Society, University of Virginia, 1(17): 349-363.

WEAVER. W. J. 1897. River adjustments in North Carolina.—Journal, Elisha Mitchell Scientific Society, 13(1): 13-24.

WHITE, W. A. 1953. Systematic drainage changes in the Piedmont of North Carolina and Virginia.—Bulletin, Geological Society of America, 64: 561-580.

WHITEHEAD, D. R. 1965. Palynology and Pleistocene phytogeography of unglaciated eastern North America, pp. 417-432. *In* Wright, H. E., Jr. and D. G. Frey (eds.). The Quaternary of the United States.—Princeton University Press, Princeton, New Jersey.

WHITWORTH, W. R., P. L. BERRIEN, and W. T. KELLER. 1968. Freshwater fishes of Connecticut.—Bulletin, State Geological and Natural History Survey of Connecticut, Number 101, 134 pp.

WILLIAMS, J. D. 1968. A new species of sculpin, *Cottus pygmaeus*, from a spring in the Alabama River basin.—Copeia (2): 334-342.

.... and C. R. ROBINS. 1970. Variation in populations of the fish *Cottus carolinae* in the Alabama River system with description of a new subspecies from below the Fall Line.—American Midland Naturalist, 83(2): 368-381.

WILLOCK, T. A. 1969. Distributional list of fishes in the Missouri drainage of Canada. Journal, Fisheries Research Board of Canada, 26(6): 1439-1449.

WILSON, C. B. and H. W. CLARK. 1914. The mussels of the Cumberland River and its tributaries.—Document, United States Bureau of Fisheries, Number 781, 63 pp.

WINN, H. E. 1958. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces-Percidae).—Ecological Monographs, 28(2): 155-191.

WOODS, L. P. and R. F. INGER. 1957. The cave, spring, and swamp fishes of the family Amblyopsidae of central and eastern United States.—American Midland Naturalist, 58(1): 232-256.

WOOLMAN, A. J. 1892. Report of an examination of the rivers of Kentucky, with lists of the fishes obtained.—Bulletin, United States Fish Commission for 1890, 10: 249-287.

WRIGHT, F. J. 1931. The Older Appalachians of the South.—Journal, Denison University Science Laboratory, 26: 143-250.

.... 1934. The Newer Appalachians of the South; Part 1, Between the Potomac and New Rivers.—Jounral, Denison University Science Laboratory, 29: 1-105.

.... 1936. The Newer Appalachians of the South; Part 2, South of the New River.—Journal, Denison University Science Laboratory, 31: 93-142.

YERGER, R. W. and K. RELYEA. 1968. The flat-headed bullheads (Pisces: Ictaluridae) the southeastern United States, and a new species of *Ictalurus* from the Gulf Coast. Coast.—Copeia (2): 361-384.

YOUNG, J. L. 1963. South Atlantic States, pp. 269-284, *In* Frey, D. G. (ed.). Limnology in North America.—University of Wisconsin Press, Madison, Wisconsin.

ZORACH, T. 1968. *Etheostoma bellum,* a new darter of the subgenus *Nothonotus* from the Green River system, Kentucky and Tennessee.—Copeia (3): 474-482.

.... 1969. *Etheostoma jordani and E. tippecanoe,* species of the subgenus *Nothonotus* (Pisces: Pecidae).—American Midland Naturalist, 81(2): 412-434.

.... and E. C. RANEY. 1967. Systematics of the percid fish, *Etheostoma maculatum* Kirtland, and related species of the subgenus *Nothonotus.*—American Midland Naturalist, 77(2): 296-322.