

# PRESENT AND HISTORICAL SPAWNING GROUNDS AND NURSERIES OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, IN THE DELAWARE RIVER<sup>1</sup>

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## ABSTRACT

Spawning occurs from late May into July but mainly in a 3-wk period from late May to mid-late June. Spawning ends progressively later proceeding upstream. Light intensity seemed to regulate when spawning began each day. Fish selected shallow riffle areas in preference to pool habitat for spawning. Spawning behavior is described.

Except for the most grossly polluted tidal water, spawning and nursery areas now extend throughout fresh water of the main Delaware and into the East and West branches. The most important spawning grounds and nurseries are now located from Port Jervis, N.Y., to Hancock, N.Y., and extend into the lower East Branch; this has probably been the case since 1910-20. There has been a fundamental upstream shift in the chief spawning grounds and nurseries since the decline of the Delaware River shad runs, because these historically extended downstream from about Delaware Water Gap, Pa., and included tidal water. Reasons for this shift suggest intrastream homing.

Only a small proportion of the historical nursery now contributes to production. Nursery and spawning areas now contribute to production of adults in proportion to their distance from Philadelphia, Pa. The extent of the spawning and nursery area since about 1910-20 has probably expanded and contracted around a core area in the upper Delaware near Hancock. Future prospects of Delaware River shad are discussed. They depend upon water quality in the tidal area and the proposed Tocks Island dam. Extirpation of the remnant runs is a distinct possibility.

The Delaware River basin once supported larger landings of American shad, *Alosa sapidissima*, than any other river system (Stevenson 1899). Annual landings near the turn of the century averaged about 14-17 million pounds but have consistently been much less than 0.5 million pounds since 1920 (Sykes and Lehman 1957; Chittenden 1974). Gross pollution near Philadelphia, Pa. (Figure 1), has been the chief reason for the low abundance since at least 1920 (Ellis et al. 1947; Sykes and Lehman 1957; Chittenden 1969). If pollution were cleared up, shad runs could be largely restored (Chittenden 1969).

Spawning and nursery areas of shad in the Delaware River are not well known, although the U.S. Army Corps of Engineers proposes to construct a dam near Tocks Island, a few kilometers upstream of Delaware Water Gap, Pa. If proposed fishways are not successful, this dam would prevent access to nearly half the 406 km of fresh water between Marcus Hook, Pa., and Hancock, N.Y. Sykes and Lehman (1957) concluded that the

chief spawning and nursery areas were located upstream of Tocks Island. Their studies were made in 1950-52 when shad runs were almost nonexistent, however, and their conclusion was necessarily based on extremely limited data. Shad runs markedly resurged during the early mid-1960's when I made extensive collections and observations of adults and young. This paper describes the spawning period, behavior during the spawning period, recent and historical spawning and nursery grounds, and discusses the future prospects of shad in the Delaware River.

## MATERIALS AND METHODS

Locations referred to are indicated in Figure 1 or, when first mentioned, by their approximate distances upstream from Marcus Hook, situated about 90 km downstream from the fall line at Trenton, N.J., and near the transition between fresh and brackish water.

Adults (278 males and 250 females) were collected during the spawning runs at Lambertville, N.J., using a 76-mm stretch-mesh, 107-m long and 3.6-m deep haul seine at 3- or 4-day intervals from 5 April to 19 May 1963, 20 March to 18 May 1964, 26 March to 7 May 1965, and 27 March to 19

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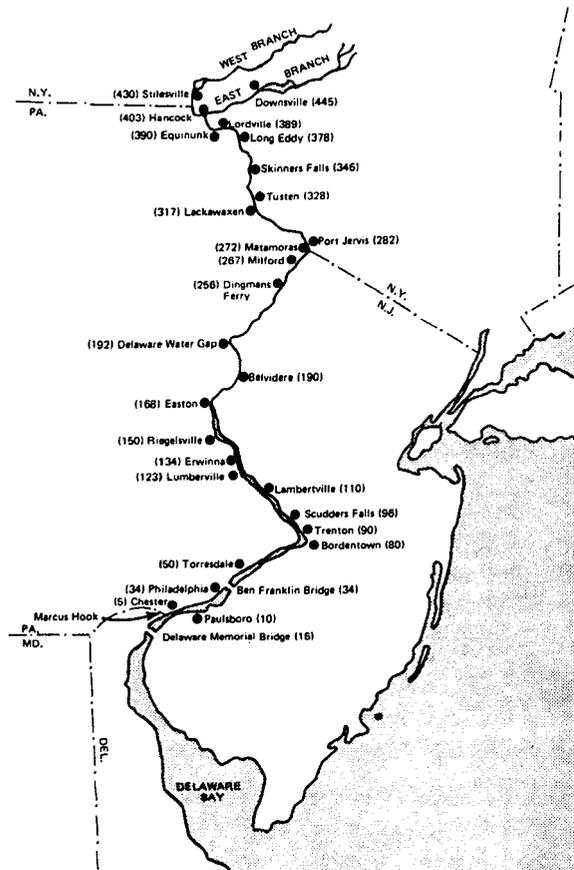


FIGURE 1.—The Delaware River. Numbers in parentheses represent distance in kilometers from Marcus Hook, Pa.

May 1966. Low dissolved oxygen near Philadelphia blocked upstream passage of part of the 1965 spawning run, and few fish were captured at Lambertville (Chittenden 1969); however, 43 dead males and 147 females were collected 21 May-10 June during a fish kill near Paulsboro, N.J. The gonads of all adults collected were examined to assess their degree of maturation following criteria of Leach (1925).

Data on the abundance of adults in the period 1959-62 were obtained from surveys (hereinafter referred to as the Tri-State Surveys) during July and August by the states of New Jersey, New York, and Pennsylvania in cooperation with the U.S. Fish and Wildlife Service. Rotenone was used to collect. After 1962 I made many observations on adult abundance and gonad condition during irregular collections upstream from Dingmans Ferry, Pa., especially during annual float trips in late May between Hancock and Port

Jervis, N.Y. Observations on behavior during the spawning period were made chiefly in the East Branch near Hancock.

Young fish were collected in nontidal fresh water from 1963 to 1966 using 12-mm stretch-mesh seines. In 1963, most collections were made from Milford, Pa., upstream into the East and West branches using a 1.8-m deep, 6-m long net or a similar 10.7-m long bag seine. Most seine hauls in 1963 captured few or no young, but a few hauls captured many fish. Quantitative comparisons of abundance were considered unreliable because of the extremely contagious fish distribution. Therefore, techniques were greatly modified in 1964. A 22.9-m long, 1.8-m deep net was paid out from a pram. Lights (900 W for 1 h) were used at night to attract young shad to the shoreline for most collections during 1964 and thereafter. Only one seine haul was made at a station when lights were used, and collection sites were near deep water.

During 1966, night seining with lights was conducted at 2-wk intervals at Lordville, N.Y., Tusten, N.Y., Dingmans Ferry, Belvidere, N.J., Riegelsville, Pa., and Scudders Falls, N.J., from 1-4 August to 27-29 September and weekly thereafter until 14 November following an unreplicated two-way (stations and collections periods) experimental design in which collections were made at each station until the young completely vacated nontidal water. No *F* tests for significant differences in abundance were possible because of the inherent nature of the study: collecting with lights made catches reliable but replication impossible; intensive seaward movement of the young by mid-late August caused a stations by collection period interaction which negated tests for main effects. Supplementary collections using lights were made during 1966 in the East and West branches and downstream from Dingmans Ferry (Table 1).

Nurseries refer herein to areas the young occupy during July and August. Data for 1963, 1964, and 1966 (after August) are presented in Chittenden (1969, tables 35, 36, 38, 39, 41).

## SPAWNING PERIOD

Nearly all spawning apparently occurred within a 3-wk period from about late May to mid-late June, although some spawning extended well into July. No fish had any translucent eggs until early May at Lambertville, and only one running

TABLE 1.—Summary of catch size ( $n$ ) and total lengths (mm) of young American shad collected during July and August 1966.

Date	Location	$n$	Mean	SD	Min	Max
July						
5	Dingmans Ferry <sup>1</sup>	129	37.8	5.30	26	51
6	Belvidere	46	40.4	7.09	32	60
7	Scudders Falls	7	41.0	10.28	28	53
17	Erwinna	0	—	—	—	—
25	Riegelsville	12	51.2	8.39	42	71
25	Scudders Falls	3	68.3	8.50	60	77
August						
1-4	Lordville	208	37.1	4.57	27	52
1-4	Tusten	516	43.5	9.22	26	80
1-4	Dingmans Ferry	193	62.1	9.67	34	82
1-4	Belvidere	83	62.9	8.19	48	90
1-4	Riegelsville	8	62.9	10.86	49	78
1-4	Scudders Falls	0	—	—	—	—
7	East Branch, Hancock <sup>1</sup>	406	—	—	—	—
7	Downsville	0	—	—	—	—
8	Fishes Eddy	2	44.0	4.24	41	47
8	West Branch, Hancock	0	—	—	—	—
15-17	Lordville	363	46.8	9.21	26	79
15-17	Tusten	367	50.8	7.51	34	76
15-17	Dingmans Ferry	1,282	67.5	8.79	42	93
15-17	Belvidere	177	65.9	8.55	46	98
15-17	Riegelsville	16	74.3	10.14	47	90
15-17	Scudders Falls	12	94.8	8.70	82	109
29-31	Lordville	526	53.4	8.64	34	86
29-31	Tusten	45	62.1	9.95	44	87
29-31	Dingmans Ferry	124	70.7	8.80	54	100
29-31	Belvidere	63	75.3	8.61	62	97
29-31	Riegelsville	1	55.0	—	55	55
29-31	Scudders Falls	0	—	—	—	—

<sup>1</sup>The listed  $n$  was estimated as about half the total catch; large amounts of detritus were mixed with the East Branch, Hancock catch, small fish were hard to find and measurements were not taken.

ripe female was captured as early as 15 May. The gonads of some dead fish collected near Marcus Hook on 21 and 23 May 1965 were nearly ripe. Three females seined at Skinners Falls, N.Y., on 3 June 1964 had partially spawned. In the East Branch near Hancock, I observed much spawning from 10 to 17 June 1964; a few adults moved into a spawning area there after dark on 1 July 1965, suggesting that some spawning occurred then. Most spawning probably occurred before late June, however, because there was a great mortality of adults by then (Chittenden 1976).

Spawning ended at a later date upstream than it did downstream based upon the minimum sizes of young captured (Table 1). Assuming a month between hatching and transformation at about 25 mm (Walburg and Nichols 1967), spawning in 1966 ended about 7 June near Scudders Falls and about 25 June near Riegelsville. At Belvidere, spawning occurred at least until early June and at Dingmans Ferry until 1 July. Spawning ended near Tusten from 1 to 15 July and at Lordville from 15 July to 1 August. Length frequencies of young in July and August 1966 (Chittenden 1969) also show that spawning ended later upstream than it did downstream. However, the spawning period probably varies slightly between years and

at different locations depending upon spawning stimuli.

The spawning period is apparently prolonged for individual fish. The ovaries of females captured near Hancock during June 1964 varied in size, many ovaries being about one-third or two-thirds the size of those from prespawning fish captured at Lambertville. This suggests prolonged spawning of individuals as Lehman (1953) concluded from egg diameter measurements.

## BEHAVIOR DURING THE SPAWNING PERIOD

During the day, behavior depended upon the habitat occupied. The nontidal Delaware consists of a sequential arrangement of shallow swift riffles and slow-moving deep pools. Shad preferred pools but were frequently observed in riffles about 0.3 m deep. Schools of fish circled slowly in the pools but often formed a V in riffles. The point of the V headed upstream or in the direction of travel and left a readily observed wake. When the school was stationary and facing upstream, the fish at the point of the V moved to the rear after about 30 s. The fish immediately behind these leaders then moved to the point. This behavior spreads energy expenditure among all members of the school and may conserve energy as would the preference for pools. Both may be important to survival. Weight loss during the spawning migration is high (Leggett 1972; Chittenden 1976), and starvation causes a large mortality on the Delaware River spawning grounds (Chittenden 1976).

Adults were observed after dark in the shallows by using a pole to suspend a lantern high in the air. The large schools typical of the day seem to disperse during the evening spawning period, because only one to three fish were usually observed. Several times a behavior was observed which may have been the spawning act: a smaller fish (male?) lined up on either side of a larger fish (female?) bringing their vents in close proximity while swimming; a brief splashing coincident with a rattling sound occurred at or near the surface; and the fish separated after a few seconds. Splashing and rattling noises were continually heard outside the lighted area. This behavior was only witnessed after dark, and it occurred in water as shallow as about 150 mm. Plankton nets were not available to collect fresh eggs to confirm

this was the spawning act. However, the vigorous splashing and noise is similar to the observations of Goode (1888) and Leach (1925) and of Leim (1924) who used plankton nets to collect newly fertilized eggs.

Light intensity seemed to regulate when spawning began each day, and the shad seemed to prefer shallow riffle areas for this activity. Few fish were observed during the day in a shallow riffle spawning site near Hancock, but many fish moved from the upstream pool to the riffle as evening approached. Concentration near the riffle occurred earlier on overcast days than on sunny days. I observed spawning only at night in general agreement with Pennsylvania (1875), Goode (1888), Leim (1924), Leach (1925), Walburg and Nichols (1967), and Marcy (1972). In contrast, Massmann (1952) found spawning at all hours in the Pamunkey River, Va., although possibly more intensively from noon to midnight. Water turbidity probably influences the effect of light in regulating the daily onset of spawning. Spawning probably tends to occur at night in clear water such as the upper Delaware, but seems to begin later during the day or occurs all day long in turbid water typical of tidal areas such as the Pamunkey River. Overcast skies apparently permit spawning to begin earlier in the day.

## SPAWNING GROUNDS

Important spawning grounds apparently extend no farther downstream than the Belvidere area. During the Tri-State Surveys, greatest numbers of adults were captured from Minisink Island to Skinners Falls, and none were captured downstream from Manunka Chunk (Table 2). Few adults were captured from Long Eddy, N.Y., upstream. However, these collections were made 10-21 July which is well after most adults move seaward or die (Chittenden 1976). Therefore, the chief spawning grounds may have been farther upstream.

Extensive observations from 1962 to 1968 generally support the Tri-State Survey collections, but in contrast they suggest that the area from Skinners Falls to the lower East Branch was extremely important. Many adults were observed 31 May-1 June 1962 from Milford to Delaware Water Gap, and 30 May-5 June 1963 from Mongaup River (km 296) to a few kilometers above Callicoon, N.Y. (km 360). In 1964, hundreds of adults were observed near Hancock and the lower East

Branch 29 May-20 June and (J. Musick pers. commun.) near Milford on 31 May. Fewer adults were observed after 1964, but they consistently appeared from Sparrowbush, N.Y. (km 286), to the lower East Branch in late May and early June.

TABLE 2. — Numbers of adult American shad captured during the Tri-State Surveys.

Station	Distance from Marcus Hook, Pa. (km)			
	1959	1960	1961	1962
East Branch, Hancock	403	0	0	5
West Branch, Hancock	403	0	0	0
Long Eddy	378	0	0	23
Skinners Falls	346	0	11	107
Mongaup Area	292	0	0	271
Minisink Island	263	30	0	160
Tocks Island	218	0	0	0
Manunka Chunk	197	—	32	40
Raub's Island	152	—	0	0
Marshall's Island	132	—	0	0
Scudders Falls	95	—	—	0
Trenton Falls	88	—	—	0

Some spawning occurs downstream of Philadelphia; however, few fish which pass Philadelphia spawn as far downstream as Lambertville. I collected a nearly spent male on 10 June 1965 at Marcus Hook. This fish undoubtedly had spawned nearby, because low dissolved oxygen would have prevented movement past Philadelphia after April (Chittenden 1969). The Lewis Fishery at Lambertville captured about 6,300 fish from 1963 to 1968, but only 21 were taken after 15 May.

Spawning extends into the lower West and East branches, especially the latter, but dams prevent movement upstream of Stilesville, N.Y., and Downsville, N.Y. Young shad (27 mm total length) were captured in the West Branch at Hancock on 9 August 1963 (Chittenden 1969, table 26). This suggests spawning there because net movement of the young is downstream. Adults were collected in the East Branch at Hancock during the 1961 Tri-State Surveys. Many occurred at least as far upstream as East Branch, N.Y. (km 430), in the runs of 1962-65 (W. Kelly pers. commun.; my observations). I observed spawning in the East Branch near Hancock in 1964 and 1965.

The adults ascend some tributaries, but it is not certain if they spawn there. A female was caught on 16 May 1961 in Big Flat Brook (km 235) about 10 km upstream from the Delaware (Anonymous 1961). Adults ascended several kilometers up the Mongaup River from 1962 to 1964 and 6 km up the Beaverkill River, an East Branch tributary (W. Kelly pers. commun.).

## NURSERIES

The chief nursery in 1966 was apparently located upstream from Dingmans Ferry and was especially centered near Tusten and Lordville (Table 1). Areas downstream from Tusten gradually decreased in relative importance. The chief nursery extended into the lower East Branch; many young were captured near Hancock on 7 August, but none were taken at Downsville and few were collected at Fishes Eddy, N.Y. No fish were captured in the West Branch near Hancock on 8 August, suggesting that the lower West Branch was an unimportant nursery in 1966.

Two seemingly aberrant catches affect interpretation of relative abundance upstream from Belvidere. The catch was small at Tusten on 30 August and very large at Dingmans Ferry on 17 August. Hundreds of young were attracted to the lights on 10 and 21 August at Tusten which agrees with the magnitude of catches on 4 and 16 August. The Tusten catch on 30 August probably reflects a seaward exodus of fish after 21 August. A plateau in size formed at Tusten by August 30 (Chittenden 1969, figure 47) when mean total length was 62 mm (Table 1). A plateau represents seaward movement of larger fish, and seaward movement of the young is probable when they reach 64 mm (Chittenden 1969:248). Mean size at Dingmans Ferry was 62 mm on 4 August and 67 mm on 17 August, so that the very large catch at Dingmans Ferry on 17 August probably reflects an influx of seaward moving young from farther upstream.

The Delaware River downstream of Belvidere appears to be a relatively unimportant nursery. Catches during July and August 1966 at Riegelsville and Scudders Falls were consistently much smaller than at stations farther upstream, and a catch at Erwinna, Pa., in July was also small. The largest catch in these 10 collections was 16 young. This is much smaller than the smallest catch in 14 collections at Belvidere, Dingmans Ferry, Tusten, and Lordville.

My collections and observations in 1963-65 generally agree with the nursery patterns of 1966. In 1963, young shad were observed and captured from Dingmans Ferry to the lower East and West branches; many were repeatedly observed and collected in the lower East and West branches at Hancock, and hundreds were observed near Matamoras, Pa., on 19 July and at Skinners Falls on 30 August. In 1964, young were captured from Erwinna upstream to Cochetton, N.Y. (km 354):

hundreds were observed or captured at Belvidere, Delaware Water Gap, Worthington Tract (km 217), Flatbrookville (km 235), Dingmans Ferry, Sparrowbush, Pond Eddy (km 301), and Cochetton. No collections were made upstream from Cochetton in 1964 except on 18 August when no young were captured using lights in the West Branch at Hancock. In 1965, young were observed or captured from Belvidere upstream to Pond Eddy; hundreds were observed and captured at Delaware Water Gap on 8 July, at Belvidere on 15 July, and at Dingmans Ferry, Sparrowbush, and Pond Eddy on 21 July. No trips were made upstream of Pond Eddy in 1965.

## GENERAL DISCUSSION

### Historical Spawning and Nursery Areas

Shad migrated 68 km up the East Branch to Shavertown (Bishop 1936) and 24 km up the West Branch to Deposit in the early 1800's (Gay 1892). A dam constructed at Lackawaxen, Pa., however, blocked access upstream after 1823 (Slack 1874; Smiley 1884; Gay 1892). Spawning grounds then extended downstream from Lackawaxen for about 70 yr until a fishway permitted upstream access in 1891 (Bean 1892, 1903).

Apparently the chief spawning grounds were historically downstream from Lackawaxen. The shad catch along the Atlantic coast is primarily age IV or older fish (Walburg and Nichols 1967). Few Delaware River shad migrate upstream until age III, and most now first do so at ages IV and V (Chittenden 1975). No records exist of size or age composition in the late 1800's-early 1900's when Delaware River landings reached their zenith, except that average weights about 1896 were 3.75 and 3.50 pounds (Stevenson 1899), 3.75 pounds (Townsend 1901), and 4.2 pounds based upon Smith's (1898) report on the numbers and pounds caught. These weights are reasonably similar to the mean weights of males (1,107 g) and females (1,737 g) captured at Lambertville from 1963 to 1965 (Chittenden 1976), so that recent Delaware River data probably closely represent the age structures near the turn of the century. Therefore, renewed access to spawning grounds upstream from Lackawaxen could not have fully affected landings until 1895 or 1896. Except for 1892, annual landings were about 13-14.5 million pounds in the period of 1889-95 and about 13.9-16.8 million pounds from 1896 to 1901 (Chitten-

den 1974). The catches in these two periods are so similar that it would appear that the Lackawaxen Dam had little effect on abundance. The chief spawning grounds may have been located even further downstream than Lackawaxen, however, because Abbott (1868) stated that shad were seldom plentiful upstream from Delaware Water Gap, and this is supported by Smiley's (1884) statement that no shad were seen farther upstream than Milford for 25 yr prior to 1872. Shad were abundant at that time (Slack 1874).

Spawning grounds could have extended downstream to about Marcus Hook, because shad spawn in fresh water (Prince 1907; Leach 1925; Hildebrand and Schroeder 1928; Massmann 1952). Consideration of preferred spawning and nursery habitat and Delaware River morphology suggests that tidal water was historically important: the existence of an extensive tidal nursery (and spawning area) immediately downstream from extensive excellent spawning grounds was probably important to the former abundance of Delaware River shad (Chittenden 1973b). However, the contemporary literature conflicts on the importance of the tidal Delaware (Pennsylvania 1897; discussion session after Meehan 1907; New Jersey 1916).

The potential importance of the tidal Delaware can be judged by comparison with other rivers. Hudson River runs are entirely produced in tidal water, because a dam constructed in 1840 at Troy, N.Y. (Cheney 1896), blocks passage of shad to nontidal water. Annual Hudson River landings were 2-4 million pounds from 1936 to 1949 and catches of about 5 million pounds have been reported (Talbot 1954). Migration of shad in the Potomac River is blocked by Great Falls, 16 km upstream from tidal water, so that most fish are probably from tidal spawning. Spawning grounds in several Virginia rivers are in tidal waters (Massmann 1952). Therefore, it appears that tidal spawning was once very important in the Delaware River, in agreement with Walford [a 1951 memorandum cited by Mansueti and Kolb (1953)] who stated that the principal spawning area once was probably a short distance above Gloucester, N.J. (km 30).

The area near Hancock apparently became an increasingly important spawning area—but eventually for reduced numbers of fish—as the Delaware River shad runs declined. Many fish again moved upstream into the East Branch after installation of the Lackawaxen fishway in 1890

(Bean 1892, 1903). Landings from 1904 to 1913, in general, were only about 3-5 million pounds and consistently have been much less than 0.5 million pounds since 1920 (Sykes and Lehman 1957; Chittenden 1974). In spite of this great decline, many shad (240-350/seine haul) were captured at Hancock until 1915 (Bishop 1936). Catches near Hancock gradually declined after 1915, and a shad fishing club captured only 60-75 fish annually after 1920 and less than 12 in some years (Greeley 1936; Bishop 1936).

Many tributaries, particularly in the tidal area, may have been used for spawning and as nurseries; but their historical importance is not clear. Adults entered many tributaries near Philadelphia (Meehan 1896; Stevenson 1899). The Lehigh and Schuylkill rivers were once famous shad streams (Gay 1892; Meehan 1896), although dams were constructed after 1820 and prevented access to these streams.

### Recent Spawning and Nursery Areas

With the probable exception of the most grossly polluted tidal areas, recent spawning and nursery areas have extended throughout fresh water of the Delaware and into the East and West branches. In general, nurseries must be at or downstream of spawning grounds, because the young begin to disperse downstream upon transformation from the post-larval stage—if not sooner (Chittenden 1969).

The chief spawning grounds and nurseries now extend no farther downstream than Belvidere. Gonad condition, the presence of few adults after mid-May, and the location of the chief nurseries, especially during early July, indicate that very little spawning occurs as far downstream as Lambertville. The Delaware between Belvidere and Philadelphia probably now serves as a nursery primarily due to downstream dispersal of the young. The importance of spawning grounds and nurseries now increases proceeding upstream from Belvidere towards Hancock. The most important spawning grounds and nurseries are located from about Port Jervis to Hancock and extend into the lower East Branch.

Tidal water near Philadelphia is no longer suitable as a nursery and probably not for spawning. Although conditions vary slightly between years, in general, the minimum daily dissolved oxygen is at or near 0 mg/liter from about mid-May through early December in the 66-km

stretch from Torresdale, Pa., to the Delaware Memorial Bridge, the most severely affected area being from Chester, Pa., to the Benjamin Franklin Bridge (Chittenden 1969). Minimum daily dissolved oxygen levels of about 2.5-3.0 mg/liter are needed to permit mere survival of shad, and this is not a reasonably normal existence (Chittenden 1973a).

Some spawning probably occurs in fresh water seaward of Philadelphia when low oxygen prevents upstream passage of part of the run. Therefore, this area would be a nursery. The area is limited in extent, however, and survival of fish may be precarious because of daily dissolved oxygen fluctuations due to photosynthesis or tidal movement of polluted water. de Sylva et al. (1962) collected larval shad, but no juveniles, in the Delaware River estuary shore zone even though the euryhaline young can and do utilize brackish nurseries (Chittenden 1973b). Production of shad seaward of Philadelphia, at best, apparently is small because landings in the Delaware Basin have been low for more than 50 yr.

The West Branch is apparently no longer an important nursery. Young shad were repeatedly collected at Hancock in 1963, but none were captured in two collections with lights in 1964 and 1966. Cold water releases from Cannonsville Reservoir, which began after summer 1963, may account for the apparent absence of young in the West Branch thereafter (Chittenden 1972). If so, the East Branch and possibly the Delaware below Hancock may be of precarious suitability for spawning and nursery purposes, because Pepacton Reservoir on the East Branch is also designed for water release from the hypolimnion.

Tributaries act as nurseries and possibly spawning grounds but are probably not important to production today in the Delaware River. Compton (1963) captured 38 young on 23 July 1962 in Big Flat Brook, nearly 1.6 km from the Delaware, and adults have been observed in several tributaries. Tributaries in nontidal water are too small to support many fish, however, except for the Lehigh River (km 168) which is dammed near its junction with the Delaware. Those in tidal water near or upstream of the Philadelphia area are dammed, affected by tidal movement of low oxygen water, or the young produced therein reach Philadelphia too early in summer or fail to successfully pass seaward (Chittenden 1969).

The present findings on spawning and nursery areas agree with Sykes and Lehman's (1957) ob-

servations and with their descriptions of unpublished findings of Cable: plankton tows were taken in May 1944 from Bordentown, N.J., to Equinunk, Pa.; the greatest concentration of eggs was above Lackawaxen and no eggs were found below Lumberville, Pa. Therefore, it would appear that the chief spawning grounds and nurseries have remained about the same for at least the last 30 yr and probably since about 1910-20.

### Areas Contributing to Successful Production of Adults

It appears that there has been a fundamental shift in the chief spawning grounds and nurseries since the decline of the Delaware River shad runs. Historically the chief spawning grounds were downstream of Delaware Water Gap and included the tidal area. These areas are now of little importance; since the decline, the chief spawning grounds have been upstream of Delaware Water Gap. The most important spawning grounds and nurseries for the last 60 yr or more have seemingly been near the Hancock area.

Implications of the shift in spawning and nursery areas include the existence of an intrastream homing tendency which brings the fish back to spawn in their general area of birth. Chittenden (1969) discussed in detail causes of the decline in abundance of Delaware River shad and why abundance has remained low. I suggested (1969:424) that the shift in spawning and nursery areas occurred because pollution near Philadelphia has selected for an upstream-spawning stock based upon the time when the young reach the Philadelphia area; fish produced farthest downstream have the greatest probability of reaching Philadelphia before dissolved oxygen improves sufficiently to permit successful seaward passage. This implies intrastream homing. Interstream homing exists in shad (Hammer 1942; Hollis 1948; Talbot and Sykes 1958; Nichols 1960), but direct evidence of intrastream homing is desirable.

Spawning and nursery areas near Hancock are apparently the key to maintenance of the remnant Delaware River shad runs, because Chittenden (1969) demonstrated that the last fish to move seaward were, in general, those produced farthest upstream. The extent of the spawning and nursery area since about 1910-20 or earlier has probably expanded and contracted depending upon the size of the run and spawning success.

Important spawning and nursery areas probably extend farthest downstream when the run is large and spawning is successful. The upper Delaware area near Hancock is probably the core around which expansion and contraction occurs.

Downstream sections of the nursery usually contribute little or nothing to production of adults even if the nursery expands. Since 1925, larger shad runs in the Delaware River have depended upon one year class which successfully passed the Philadelphia area (Chittenden 1975). Downstream nurseries contribute to production only when water quality near Philadelphia permits shad passage earlier than normal; there is usually catastrophic destruction of the young as they pass Philadelphia (Chittenden 1969). Therefore, in general, it appears that nursery and spawning areas contribute to production in proportion to their distance from Philadelphia. Only a small part of the historical nursery area now contributes to production of adults.

### Future Prospects

Future prospects of shad in the Delaware River depend primarily upon water quality in the tidal area and upon a dam near Tocks Island (Chittenden 1969). The present remnant runs appear based upon stocks that spawn far upstream in a small part of their former spawning grounds and whose progeny pass tidal water in late fall when dissolved oxygen increases. A greater area would contribute to successful production if dissolved oxygen increased earlier, because fish spawned farthest downstream pass tidal water first. Therefore, the magnitude of future runs will reflect dissolved oxygen conditions, because the area contributing to production will change accordingly. If recent or typical water quality was maintained, future runs would usually be small. Fortuitous circumstances would occasionally produce larger runs as in the early 1960's.

Construction of a dam near Tocks Island would greatly affect shad. They probably would be extirpated from the Delaware if successful fishways for both adults and young are not provided and water quality in the tidal area is unchanged. Cold water reservoir releases drastically and adversely affect usage of downstream spawning and nursery areas, if only due to avoidance (Chittenden 1972). Cold water releases from a Tocks Island dam would shift spawning and nursery areas far downstream, and spawning grounds

under any water release circumstances would be downstream of the area that presently produces adults successfully. Therefore, the young produced would reach tidal water too early to pass seaward successfully. Great water quality improvement would be needed in the tidal area just to maintain the present small runs. Water quality improvement by flow augmentation might be self-defeating, because the young now move downstream even during the summer; and increased discharge and temperature decrease would accelerate this. The potential would be brighter if successful fishways were provided. The reservoir might be an excellent nursery for the young judging from their pelagic habits, their preference for pool habitats, and the former importance of tidal nurseries. This, combined with nurseries upstream from the reservoir, might establish larger runs—if the young passed the dam and tidal water successfully. However, much larger runs would be achieved with less risk at possibly less cost if Delaware River water quality in the tidal area were restored and the dam was not built. Then, the outstanding recreational potential of a clean tidal area in a great population center would be restored—and the outstanding recreational opportunity of an unobstructed Delaware River would not be lost.

### ACKNOWLEDGMENTS

For assisting in collections, I am deeply grateful to J. Westman and J. Hoff, J. Harakal, D. Riemer, J. Barker, F. Bolton, R. Coluntuno, K. Compton, R. Gross, C. Masser, R. Stewart, J. Miletich, S. Hoyt, L. Schulman, H. Dinje, H. Buckley, J. Musick, M. Bender, J. Gift, C. Townsend, R. Bogacz, and K. Marcellus of or formerly of Rutgers University, Harvard University, the New Jersey Division of Fish and Game and/or the New York Department of Environmental Conservation.

Fred and William Lewis, Jr. generously gave permission to collect at their fishery at Lambertville and frequently assisted in seining. W. Kelly of the New York Department of Environmental Conservation and J. Musick, then at Harvard University, provided observations. J. McEachran and R. Noble of Texas A&M University reviewed the manuscript.

The U.S. Bureau of Sport Fisheries and Wildlife, New Jersey Division of Fish and Game, Pennsylvania Fish Commission, and New York Department of Environmental Conservation

kindly permitted use of data collected during the Tri-State Surveys of the Delaware River. Financial support was provided, in part, by Rutgers University, The Sport Fishing Institute, Delaware River Basin Commission, and U.S. Public Health Service.

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