DYNAMICS OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, RUNS IN THE DELAWARE RIVER[1]

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ABSTRACT

Adult American shad were collected by haul seining at regular intervals during the spring migrations from 1963 to 1965 and by collecting specimens from a fishkill in spring 1965. Supplementary sex and size composition data were obtained from summer rotenone sampling in 1961 and 1962.

Males tended to precede females in the spring run. Annual sex compositions were strongly male dominated from 1961 to 1963 and were strongly female dominated in 1964 and 1965. Repeat spawners composed 2.6% of 729 fish examined from 1963 to 1965. Age I and II fish were absent or virtually absent from the run. Males migrated upstream primarily at age IV and females at age V. Large runs during the early 1960's were based on the 1958 and 1959 year classes as defined which were much larger than other year classes produced in the period 1957-64. Delaware River American shad runs now have little buffering against fluctuations in abundance because few year classes are successful, few age groups support the run, and there are essentially no repeat spawners. Larger runs in the Delaware since 1925 and probably somewhat earlier, in general, were apparently based on one large year class and essentially no repeat spawners.

The American shad, *Alosa sapidissima*, formerly was one of the most abundant anadromous fishes in the United States where more than 50 million pounds were landed in 1896. In contrast, only 8 million pounds were caught in 1960 (Walburg and Nichols 1967). Much of this decline is due to the collapse of the Delaware River Basin fisheries which once supported larger landings of American shad than any other river system (Stevenson 1899). Estimates of the 1896 Delaware Basin catch are about 16.5 to 19.2 million pounds (Smith 1898; Sykes and Lehman 1957; Walburg and Nichols 1967)—about a third of the national total. Annual Delaware Basin catches about that time varied from 14 to 17 million pounds and were probably primarily fish of Delaware River origin (Chittenden 1974). In contrast, annual Delaware Basin landings since 1920 have consistently been much less than 0.5 million pounds (Sykes and Lehman 1957; Chittenden 1974).

Trends in abundance of Delaware Basin stocks have been described by Sykes and Lehman (1957) and Chittenden (1974), and causes of these fluctuations have been described by Ellis et al. (1947), Sykes and Lehman (1957), Walburg and Nichols (1967), and Chittenden (1969). The dominant factor affecting abundance during the past 60 yr, at least, has been pollution near Philadelphia, Pa. Complete understanding of the causes of fluctuations in abundance, however, depends on detailed knowledge of the population dynamics of this species. Many workers have described certain aspects of the population dynamics of American shad in other river systems. Little work has been published for the Delaware, in part because Delaware River American shad stocks have been so low that it has been difficult to collect large numbers of fish.

The present paper describes data collected on sex, size, age, and repeat spawner composition; comparative magnitudes of American shad runs; and year-class strengths in the Delaware River during the late 1950's and the 1960's.

MATERIALS AND METHODS

Adult fish were collected 22.5 km (14 miles) above tidal water in the years 1963 to 1965 at the site of the Lewis Fishery in Lambertville, N.J., using a 76-mm (3-inch) stretch-mesh, 107-m (350-foot) long and 3.6-m (12-foot) deep (4.3 m = 14 feet in 1963) haul seine that was paid out from a boat and landed about 396 m (1,300 feet) downstream. Sampling occurred at 4-day intervals after a randomly selected date in 1963 but at fixed intervals

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twice weekly in later years. Sampling occurred from 5 April to 19 May in 1963, from 20 March to 18 May in 1964 and from 26 March to 7 May in 1965. In 1964 and 1965, at least, several collections were made both before and after the first and last American shad were captured, but a few fish were captured on the first and last sampling dates in 1963. My sampling in 1963 essentially ended when the run did at Lambertville. I captured 1 fish after 15 May, and the Lewis Fishery captured 5 fish after that date of a total catch of about 4,000 fish (Chittenden 1969). The number of seine hauls and time of sampling varied each day during 1963. After 1963 two seine hauls were made from 1100 to 1300 EST on each sampling day after the first American shad was landed. In spring 1965, low dissolved oxygen levels near Philadelphia blocked upstream passage of part of the spawning run, and few fish were captured at Lambertville (Chittenden 1969). Hundreds of dead fish were collected during a fishkill seaward of Philadelphia in the area from Paulsboro, N.J., to Marcus Hook, Pa., during the period from 21 May to 10 June. Sex and size composition data for 1961 and 1962 were obtained from cooperative surveys (hereinafter referred to as the Tri-state Surveys) using rotenone during July and August by the states of New Jersey, New York, and Pennsylvania in conjunction with the U.S. Fish and Wildlife Service. I personally examined many of the American shad collected.

Each fish collected after 1962 was measured and was sexed by examination of the gonads, and scales were taken from the midline of the left side below the dorsal fin following Cating (1953) or from the same area on the right side. Many fish collected near Marcus Hook during 1965 had lost all or nearly all their scales, so scales were taken where available on these fish. Scales selected for age determination were cleaned and were dry-mounted between glass slides. Aging was done with a microprojector using Cating's (1953) method which was verified by La Pointe (1958) and Judy (1961). Scales were examined in the time sequence 1963, 1964, and 1965 for an initial determination. Many of the large fish were known to have been misaged when the sequence was completed. Scales were next thoroughly mixed to remove bias due to knowledge of the collection year and were reread. The first two readings disagreed on 31 of 301 fish (10%) from 1963, 38 of 199 (19%) from 1964, and 3 of 184 (2%) from 1965. Of these, 32 disagreements were on females reassigned from age-group V to VI (9 from 1963 and 23 from 1964). A third examination of the misaged scales agreed with the second on 67 of the 72 fish. The remaining 5 were discarded.

RESULTS AND DISCUSSION

Sex Composition of the Spawning Runs

Many American shad were captured at Lambertville during 1963 (301 fish) and 1964 (199 fish). Figure 1 shows trends in the cumulative percentage of males as these spawning runs progressed. Trends were similar during each year although the 1963 run contained a much higher percentage of males than the 1964 run. The cumulative proportion of males decreased as the run progressed in agreement with the observations or statements of many workers including Stevenson (1899), Prince (1907), Leach (1925), Hildebrand and Schroeder (1928), Nichols and Tagatz (1960), and Walburg and Nichols (1967).

Annual sex compositions of the runs from 1961 to 1965 are presented in Table 1 with 95% confidence limits for the proportion of males based upon normal approximations except for 1962 when a Poisson approximation to the binomial was used (Cochran 1953). Annual sex composition varied greatly from 1961 to 1965. It was male dominated from 1961 to 1963 and female dominated thereafter.

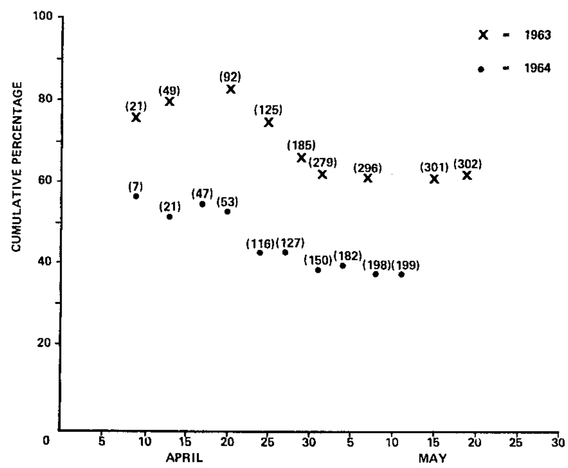

FIGURE 1.—Trends in the cumulative percentage of male American shad. Numbers in parentheses represent cumulative numbers of fish captured.

TABLE 1.–Annual sex compositions of American shad runs, 1961-65.

Year	Sample size (n)	Proportion male (p)	95% CL about p[1]
1961	198	0.86	0.81-0.94
1962	220	0.99	0.96-1.00
1963	302	0.62	0.57-0.67
1964	199	0.38	0.31-0.45
1965 Lambertville	23	0.52	0.32-0.72
1965 Tidal area	190	0.23	0.17-0.29

[1]Confidence limit for proportion of males.

Size Composition

Mean fork lengths, numbers of fish, 95% confidence limits for means, and 99% limits for individuals collected at Lambertville or the tidal area and during the Tri-state Surveys are summarized in Table 2. Data were originally expressed in total or fork length depending on year of collection. Means and confidence limits were transformed to fork lengths in inches using the regression of fork on total length presented by Chittenden (1969) and were then transformed to metric units. Females from Marcus Hook and Lambertville did not appear significantly different in size and were pooled. Males from Marcus Hook were significantly smaller (t = 4.67) than those from Lambertville, and they were not combined.

Fish were smaller in 1961 and 1962 than in later years, and this probably reflects the presence of very young individuals of the strong 1958 and 1959 year classes (see section "Comparative Year-Class Strengths"). Females averaged about 50 mm (2 inches) longer than males each year. Confidence limits for individuals indicate that there were few females longer than 545 mm (21.5 inches) and few males longer than 505 mm (19.9 inches). Maximum observed sizes were 559 and 495 mm (22.0 and 19.5 inches) for females and males, respectively. Small fish did not migrate upstream. The smallest female was about 64 mm (2.5 inches) longer than the smallest male each year. There were few females shorter than 416 mm (16.4 inches) in 1963, 1964, and 1965, the smallest being 406 mm (16.0 inches). The smallest female observed was 376 mm (14.8 inches) and 391 mm (15.4 inches) in 1961 and 1962, respectively. Confidence limits indicate that there were few males shorter than about 337 mm (13.2 inches) from 1962 to 1965. There were few males shorter than 289 mm (11.4 inches) in 1961, the smallest fish measured being 269 mm (10.6 inches).

Age and Repeat Spawner Comsposition

There were only 2.6% repeat spawners in 729 fish examined from 1963 to 1965. Annual occurrences were 1 of 299 fish (0.3%) in 1963, 3 of 199 (1.5%) in 1964, and 15 of 231 (6.5%) in 1965. Confidence limits for the annual percentages are 0.0 to 1.9% (1963) and 0.03 to 4.4% (1964) based upon Poisson approximations and 3.5 to 9.5% (1965) based upon the normal approximation.

Table 3 summarizes male and female age-class structures of the 1963 and 1964 runs at Lambertville, pooled data for 1965 from Lambertville and Marcus Hook, and data pooled over all years. Fluctuations in age composition due to variable year-class recruitment are apparent, but certain general features of the age composition stand out.

TABLE 2.–Summary of fork lengths of American shad, 1961-65. Lengths are in millimeters (top rows) and inches (bottom rows).

Year	Males				Females			
	n	Mean ($\bar{x}$)	95% CL $\bar{x}$	[2]99% CL x	n	Mean ($\bar{x}$)	[1]95% CL $\bar{x}$	[2]99% CL x
1961	170	401	394-407	289-512	28	452	441-463	371-533
		15.8	15.5-16.0	11.4-20.1		17.8	17.4-18.2	14.6-21.0
1962	217	415	414-415	362-467	3	451	322-579	—
		16.3	16.3-16.3	14.2-18.4		17.8	12.7-22.8	—
1963	186	428	425-431	371-485	115	472	468-476	416-529
		16.9	16.7-17.0	14.6-19.1		18.6	18.4-18.8	16.4-20.8
1964	76	427	420-434	350-504	122	480	477-484	428-533
		16.8	16.6-17.1	13.8-19.8		18.9	18.8-19.1	16.9-21.0
1965	12	436	417-455	342-530	11	483	472-495	431-536
Lambertville		17.2	16.4-17.9	13.5-20.9		19.0	18.6-19.5	17.0-21.1
1965	43	417	408-426	337-498	147	484	480-488	422-546
Tidal area		16.4	16.1-16.8	13.2-19.6		19.1	18.9-19.2	16.6-21.5
1965	—	—	—	—	158	484	481-488	423-545
Combined		—	—	—		19.1	18.9-19.2	16.7-21.5

[1]Confidence limit for mean fork length.
[2]Confidence limit for indivdual fish collected.

TABLE 3.—Age-class structures of American shad, 1963-65.

Age	1963 n	1963 %	1964 n	1964 %	1965 n	1965 %	Total n	Total %
				Males				
II	0	0	1	1	0	0	1	0.00
III	4	2	1	1	3	6	8	2.58
IV	149	82	51	68	36	68	236	76.13
V	27	15	21	28	14	26	62	20.00
VI	2	1	1	1	0	0	3	0.01
				Females				
IV	31	27	9	7	10	8	50	13.70
V	63	56	77	64	85	65	225	61.64
VI	19	17	35	29	34	26	88	24.11
VII	0	0	0	0	2	2	2	0.01

The following comments essentially apply to virgin fish because the percentage of repeat spawners was negligible.

Age I and II males did not migrate upstream, although one age II male was captured in 1964. Few age III males migrated upstream, the percentage based on pooled data over all years being less than 3%. Males migrated upstream primarily at age IV (76%), but age V (20%) was also important. Few males survived to age VI, and all were virgin. No males older than age VI were captured. No females younger than age IV or older than age VII were observed. Only two age VII females (less than 1% of the pooled total) were captured, and one of these was a virgin. Females were primarily age V (62%) when they first entered the fishery, but ages IV (14%) and VI (24%) were also important.

Comparative Magnitudes of American Shad Runs, 1961-68

I here define magnitude of American shad runs as the numbers of adults reaching Lambertville on their upstream migration. The magnitude of runs as defined is influenced by year-class strength as later defined herein and by dissolved oxygen levels that the adults encounter during migration upstream past the Philadelphia area (Chittenden 1969). Chittenden examined in detail the annual effects of oxygen upon passage of adults and young. In general, dissolved oxygen is sufficiently high that the earlier stages, at least, of the adult run successfully migrate upstream.

Reasonably precise estimates of the comparative magnitudes of American shad runs in the 1960's are available from three sources of evidence: 1) catches of the Lewis Fishery at Lambertville presented by Chittenden (1974), 2) my own catches at Lambertville, and 3) sex compositions of the runs presented in Table 1.

Lewis Fishery annual catch/seine haul records indicate the comparative magnitudes of runs in descending size order were: 1963 (56.1 fish), 1964 (18.3), 1962 (13.9), 1965 (6.6), 1967 (3.7) = 1961 (3.5), and 1966 (1.8) = 1968 (1.2). Values in parentheses represent catch/seine haul. My annual catch/seine haul at Lambertville for the time period between capture of the first and last fish was 17.4 fish in 1963, 9.0 in 1964, and 3.0 in 1965, a pattern in agreement with the Lewis Fishery records. My general impressions derived from angling experience, interviews with other anglers, and visual observations of the abundance of adult American shad during extensive float trips each year from 1961 to 1974 are in general agreement with the patterns suggested by the Lewis Fishery records. Runs were much smaller from 1966 to 1968 than from 1962 to 1964. The size of the run in 1965 (and possibly 1961 based on my general impressions) was intermediate between the sizes in these two periods.

The relative magnitudes of runs estimated from sex composition data (Table 1) agree with patterns indicated by catch records at Lambertville. The sex ratio shift from 1963 to 1964 suggests passage through the fishery of a year class stronger than the one immediately following because males tend to enter the run a year earlier than females. This indicates the 1963 run was larger than that in 1964.

The male proportion at Lambertville in 1965 (0.52) is biased towards the high side because the later part of the run was blocked by low dissolved oxygen near Philadelphia. The male run was much greater in 1963 than in 1964. Confidence limits for the male proportion of fish collected at Marcus Hook in 1965 were much lower than any single daily male proportion in 1963 (Figure 1) but were similar to the lowest daily male proportion in 1964. Therefore, the 1965 run was probably similar in sex composition to that of 1964. Females enter the run a year older than males. Unless females suffer a much lower annual mortality, similarity of sex compositions suggests that the 1965 run was smaller than the 1964 run—even before the fish reached the Philadelphia area. The high female proportion in 1965 suggests an even smaller run was due in 1966, another year when low oxygen levels blocked part of the run (Chittenden 1969). Dissolved oxygen was sufficiently high throughout the 1967 run to permit large numbers of fish to reach Lambertville (Chittenden 1969). The Lewis Fishery in 1967 did not make large catches to reflect 1968 males or females associated with the

1966 males, suggesting that the 1966 and 1968 runs were small—even before the fish reached the Philadelphia area.

The higher proportion of males in 1962 than in 1961 indicates that the 1962 run was larger than the 1961 run.

Comparative Year-Class Strengths, 1956-64

I here define year-class strength as the numbers of young which exist at some constant point in time—say 1 January—after the entire year class has "passed" seaward through the grossly polluted Philadelphia area. Year-class strength is influenced by spawning success. However, the dominant factor, by far, in setting year-class strength in the Delaware River is the success with which the young pass seaward through the Philadelphia area in summer and fall (Chittenden 1969).

Comparative year-class strengths can be estimated from the age and sex compositions from 1963 to 1965 (Tables 1, 3) supported by estimates of comparative run sizes. Males usually first migrate upstream at age IV and females at age V, so that the size of a run chiefly reflects the strength of year classes produced 4 and 5 yr earlier assuming constant survival at sea. Therefore, American shad runs from 1961 to 1968 chiefly reflect year-class strengths from 1956 to 1964. The largest year classes as defined were produced from 1957 to 1960 because the largest runs were from 1962 to 1964.

The 1963 American shad run was the largest in this period and primarily reflects the 1958 and 1959 year classes. I captured 90 age V fish at Lambertville in 1963 and 98 in 1964 with approximately equal effort, suggesting that the 1958 and 1959 year classes were similar. This agrees with comparative magnitude estimates for the 1962 and 1963 runs. The 1963 run was based on two large year classes and was larger than the 1962 run which was based on one large and one smaller year class.

The 1960 and 1959 year classes can be compared. I collected 180 age IV fish at Lambertville in 1963 but only 60 age IV's in 1964. This suggests that the 1959 and, by inference, 1958 year classes were much larger than that of 1960. This deduction is supported by the shift in sex composition from 1963 to 1964, which indicates the age V year class from 1959 was much stronger than the age IV year class from 1960. The 1963 run was based on two large year classes and was larger than the 1964 run which was based on one large and one smaller year class.

The 1957 and 1958 year classes can be compared. At Lambertville, 36 and 21 age VI fish were captured in 1964 and 1963, respectively, suggesting that the 1958 and, by inference, 1959 year classes were stronger than that of 1957. This is supported by mean sizes of males collected during the Tristate Surveys of 1961 and 1962 (Table 2). The 1961 fish (mean = 401 mm = 15.8 inches) were significantly smaller than the 1962 fish (mean = 414 mm = 16.3 inches). The observed mean fork length of age IV males in 1963 and 1964 was about 422 mm (16.6 inches) (Chittenden 1969, table 17), suggesting that age III fish from 1958 were important in the 1961 run.

The 1961 and 1960 year classes can be compared. Sex composition and catch data show that the 1964 run was smaller than the 1965 run. Age structures were almost identical, however, and this indicates that the 1961 year class was smaller than that of 1960.

The strength of the 1962, 1963, and 1964 year classes as defined must have been small, probably being no larger than the 1961 year class, because the 1966 to 1968 runs were very small.

In summary, the 1958 and 1959 year classes were extremely large in comparison to the year classes produced in the period 1961-64. The 1957 and 1960 year classes were much smaller than those of 1958 and 1959, but were larger than the 1962, 1963, and 1964 year classes.

GENERAL DISCUSSION

Delaware River American shad runs in the 1960's showed great shifts in the proportion of male fish. This variation was due, in large part, to fluctuations in year-class strength. The proportions in 1961 (0.86) and 1962 (0.99) are extreme. They are based upon summer collections and are biased if females tend to return seaward earlier than males do. However, these proportions also probably primarily reflect the temporary resurgence of the Delaware River American shad runs in the early 1960's reported by Chittenden (1974). The magnitude of American shad runs in the Delaware River was at a very low level prior to 1961, increased in 1961 and 1962, and in 1963 the magnitude was such that it ranked among the largest runs in the last 45 yr or more. Because Delaware River males tend to undertake their first spawning migration at age IV and females at age V, the strongly male dominated runs of 1961 and 1962 reflect the entry of unusually large year classes into the fishery. The magnitude of the spawning runs declined greatly after 1963, and the shift towards female dominance reflects the failure of new year classes to be recruited. The strength of the 1962, 1963, and 1964 year classes as defined was small because the 1966 to 1968 runs were very small. Yet, from visual observations and collections of young during the summer, Chittenden (1969) concluded that strong year classes were produced throughout the period 1962-66. I presented dissolved oxygen data for the periods when the young passed the Philadelphia area each year and ascribed the failure of these strong year classes to later recruit to the fishery to catastrophic destruction of the young as they passed through the grossly polluted area.

There was a negligible percentage of repeat spawners in the Delaware River American shad runs from 1963 to 1965, and there were no repeat spawners among 245 American shad collected from the 1961 run (J. Malcolm, pers. commun.). The existence of numerically few repeat spawners must have continued to be the case after 1965 because the runs from 1966 to 1968 were very small. Delaware River runs apparently have included few repeat spawners for at least some 25 yr because Sykes and Lehman (1957) reported that less than 2% of 423 fish captured in 1944, 1945, 1947, and 1952 were repeat spawners. Even the production of very large year classes appears to have little effect on the percentage of repeat spawners in the Delaware River. The percentage was only 6.5% in 1965, a year when the very strong 1958 and 1959 year classes should have increased the percentage greatly rather than by only a few points. As Sykes and Lehman (1957) pointed out, the virtual absence of repeat spawners in the Delaware River is very unlike that in other middle-North Atlantic coast rivers where repeat spawner percentages have been: St. Johns River, N.B., Canada, 22-81% (Leggett 1969); Connecticut River, 14-60% (Moss 1946; Nichols and Tagatz 1960; Leggett 1969); Hudson River, 51% (Talbot 1954); Susquehanna River, 37% (La Pointe 1958); Potomac River, 17% (Walburg and Sykes 1957); York River, 21-27% (Nichols and Massmann 1963; Leggett 1969); James River, 27%, (Walburg and Sykes 1957). Some of the higher percentages of repeat spawners in these rivers are undoubtedly biased towards the high side because they are based on collections of fish from hightly selective commercial gill nets. However, it appears that the Delaware River has a much lower percentage of repeat spawners. The Delaware River seems most like rivers south of Cape Hatteras, N.C., where few repeat spawners have been reported: Neuse River, less than 3% (La Pointe 1958; Walburg 1957); Edisto River, 0% (Walburg 1956); Ogeechee River, 0% (Sykes 1956); Altamaha River, 0% (Godwin and McBay 1967; Godwin 1968); St. Jones River, Fla., 0% (Walburg 1960; Leggett 1969).

Age-class structures of American shad runs have been reported by many workers including Talbot (1954), Fredin (1954), Walburg (1956, 1957, 1960, 1961), Walburg and Sykes (1957), Sykes (1956), La Pointe (1958), Nichols and Tagatz (1960), Nichols and Massmann (1963), Godwin (1968), and Leggett (1969). Walburg and Nichols (1967) summarized the available information by stating that age IV and V fish make up the bulk of the catch in South Atlantic rivers and Chesapeake Bay tributaries while the catch is primarily composed of age IV to VII fish in middle Atlantic rivers. Delaware River runs in the 1960's were primarily supported by age IV and V fish, although age VI females were also important. Sykes and Lehman (1957) reported similar findings for fish collected in the 1940's and 1952 except that they gave more weight to age VI fish, possibly due to sampling with commercial gill nets.

Because of the absence of repeat spawners, which tend to be older fish, few age-groups support American shad runs in the Delaware River. This is similar to the situation in South Atlantic rivers but unlike that in North Atlantic rivers. The apparent similarity of Delaware River American shad to those of southern rivers rather than to geographically more closely related fish from northern rivers is an artifact caused by man. Howell (1837) reported that American shad captured in the Delaware River averaged about 3,175 g (7.00 pounds). In contrast, Chittenden (1969) reported that males averaged 1,107 g (2.44 pounds) with 95% confidence limits about the mean being 1,080-1,134 g (2.38-2.50 pounds) and females averaged 1,737 g (3.83 pounds) with the 95% confidence limits being 1,701-1,774 g (3.75-3.91 pounds). The older age-classes obviously present in Howell's time are now absent, primarily due to pollution and fishing activities. Sykes and Lehman (1957) and Chittenden (1969) attributed the virtual absence of repeat spawners to mortality of adults in low oxygen water near Philadelphia as they migrate seaward after spawning. Added to this is a large postspawning mortality in nontidal water (Chittenden 1969). Fishing, in general, decreases the age of the stock exploited. The historical and recent effect of fishing on Delaware River stocks is not completely clear, but this was probably a much more important factor before 1910 when commercial landings were as high as 14 to 17 million pounds annually (Sykes and Lehman 1957; Chittenden 1974). White et al. (1969) tagging studies suggested that in recent years the fishing rate was probably 20%.

The larger runs in the Delaware River in the early 1960's appear to have been primarily based upon one large year class except in 1963, when two large year classes were involved. Because few age-classes and only one year class support the run each year, Delaware River American shad stocks have little buffering against fluctuations in abundance due to adverse natural or man-made environmental factors. Large fluctuations, in fact, do appear in the catch records of the Lewis Fishery since 1925 (Chittenden 1974, fig. 3). The Lewis Fishery records show large runs over a 1- or 2-yr period intermixed with stable periods when the run was of small magnitude. This is the pattern which would be expected when the fishery is supported by one year class in which males tend to enter the fishery a year before the females and there are essentially no repeat spawners. Therefore, it appears probable that sine 1925, at least, larger runs in the Delaware River have been based upon one large year class and essentially no repeat spawners.

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