WEIGHT LOSS, MORTALITY, FEEDING, AND DURATION OF RESIDENCE OF ADULT AMERICAN SHAD, *ALOSA SAPIDISSIMA*, IN FRESH WATER[1]

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ABSTRACT

Linear regression equations are given for each sex for the regressions of total weight, somatic weight, and gonad weight on length prior to spawning, and for total weight on length after prolonged stay in fresh water.

Most shad began to return seaward by late June and probably had spent a maximum of about 2 mo in fresh water. Many fish, however, remained near the spawning grounds well into summer; and many died near the spawning grounds, probably from starvation. Opportunistic feeding occurred on "planktonic" items, but adult shad do not regularly obtain energy sufficient to maintain their weight in fresh water. Weight loss was related to sex and increased with increasing size. Mean length males and females averaged 45 and 57% total weight loss, respectively. Daily somatic weight loss was at least 5.75 g for males of average size and 12.47 g for females.

The anadromous American shad, *Alosa sapidissima,* an important commercial and sport fish, ranges widely on the Atlantic and Pacific coasts of North America. There is much literature on this fish, but little of it pertains to adults in fresh water, except for aspects of their spawning and population dynamics. In the course of other studies on the Delaware River from 1960 to 1968, I made many opportunistic observations on weight loss, mortality, feeding behavior, and duration of residence of adult shad on their spawning grounds in fresh water. This paper summarizes those observations and presents data on total-fork length conversion, regressions of total weight, somatic weight and gonad weight on length prior to spawning, and regressions of total weight on length after spawning.

MATERIALS AND METHODS

Adult shad were collected during their spawning runs at Lambertville, N.J., 22.5 km above tidal water (but far downstream of the present-day spawning grounds) using a 76-mm stretch-mesh, 107 m long and 3.6 m deep haul seine that was paid out from a boat and landed about 400 m downstream. Sampling occurred at 3- or 4-day intervals from 5 April to 19 May 1963, from 20 March to 18 May 1964, from 26 March to 7 May 1965, and from 27 March to 19 May 1966. Data for the period 1959-62 were obtained from rotenone 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.

I examined grossly the stomach contents of many adults captured during the Tri-State Surveys in mid-July 1961, most of the 526 fish collected at Lambertville and many fish captured on the spawning grounds after 1962.

Length and total weight were determined on most fish in 1961 and 1962 and on all fish thereafter. Gonad weight was measured after 1962. Length, always taken in inches, was measured as fork length during 1961 and 1962 and as total length thereafter. To develop conversion factors, both measurements were taken on 490 adults collected at Lambertville during 1963 and 1964 and on 100 young captured in summer 1966. Total weight was measured in pounds (to the closest 0.1 lb) during 1961-63 but in grams thereafter. Gonad weights were always taken in grams (to the closest 0.1 g). All measurements were converted to grams, millimeters, and fork lengths for presentation herein.

Regression analyses and related statistics were calculated using computer program BMD-03R (Dixon 1967). All regressions presented herein were significant at α = 0.005. The coefficient of

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determination (Steel and Torrie 1960) was used to estimate the amount of variation in y associated with variation in x. Residuals were used to examine the data for differences due to categories of classification such as year of collection. Size ranges are given within which regressions were linear.

When first referred to, locations are followed in parentheses by their approximate distances in kilometers upstream from Marcus Hook, Pa., which is situated about 90 km downstream from the fall line at Trenton, N.J. and near the transition between brackish and fresh water.

RESULTS AND DISCUSSION

Total and Fork Length Conversion

The relationship between total length (TL) and fork length (FL) for 590 young and adult fish was linear, and 99.96% of the variation in one measurement was explained by variation in the other. Regression equations were FL = 1.28 + 0.88 TL and TL = 1.00 + 1.13 FL. Extreme deviations from regression were about ±7.6 mm for adults and less for young. The slope of the regression of fork length on total length coincides with La Pointe's (1958) factor of 0.894 to convert total length to fork length.

Total Weight-Length Relationships Prior to Spawning

The relationships between total weight (TW) and length determined for fish captured at Lambertville were TW = 1,106.77 + 8.09 (FL - 427.98) for 268 males and TW = 1,737.26 + 11.54 (FL - 476.71) for 244 females. About 81% (males) and 78% (females) of the variation in total weight was associated with variation in length. Valid ranges for linear interpolation were about 330-520 mm for males and 410-550 mm for females.

The observed arithmetic mean weights with 95% confidence limits were 1,107 ± 36 g for males and 1,737 ± 45 g for females. The smallest males were 272 and 680 g and the smallest female was 1,089 g. The heaviest male and female fish were 1,905 and 2,585 g, respectively.

Somatic Weight-Length Relationships Prior to Spawning

The relationships between log somatic weight (SW) and length determined for 85 males and 130 females captured at Lambertville in 1964 and 1965 were $\log_{10}$ SW = 3.0047 + 0.0036 (FL - 428.20) for males and $\log_{10}$ SW = 3.1807 + 0.0029 (FL - 480.73) for females. About 91% (males) and 81% (females) of the variation in log somatic weight was associated with variation in length. Valid ranges for linear interpolation were about 360-500 mm for males and 410-540 mm for females. Mean somatic weights with 95% confidence limits were 1,011 ± 56 g for males and 1,516 ± 38 g for females.

Gonad Weight-Length Relationships Prior to Spawning

The relationships between log total gonad weight (TGW) and length determined for 267 males and 244 females captured at Lambertville were $\log_{10}$ TGW = 1.8633 + 0.0033 (FL - 428.43) for males and $\log_{10}$ TGW = 2.3892 + 0.0024 (FL - 476.93) for females. Valid ranges for linear interpolation were about 330-520 mm for males and 410-550 mm for females. About 45% (males) and 26% (females) of the variation in log total gonad weight was associated with length variation. Much variation in gonad weight, especially for females, is not explained by the regression equations. Much gonad development occurs during the spawning run (Chittenden 1969), and residual plots suggested that gonad weights were heavier in 1963 than in 1964. These factors account for some unexplained variation in gonad weight.

Mean total gonad weights with 95% confidence limits were 73 ± 7 g for males and 245 ± 22 g for females.

Duration of the Freshwater Residence

Most fish begin to return seaward by about late June. I observed hundreds of adults near Hancock, N.Y. (403) until 17 June 1964, but very few were present on 14 July. Most fish had died or migrated seawards during the interim period. Delaware River shad runs begin in early April at Lambertville and the peak occurs about 1 May, depending upon the degree of pollution near Philadelphia (34) (Chittenden 1969). This suggests most fish probably spend a maximum of 2 mo in fresh water before returning seaward, in agreement with Bean's (1892, 1903) observations.

Many fish remain near the spawning grounds well into summer. The Tri-State Surveys captured many adults during midsummer between Skinners Falls, N.Y. (348) and Minisink Island, N.J. (266): 538 fish were captured at three stations in mid-July 1961; 237 fish were captured at two stations in mid-July 1962; 30 adults were captured near Milford, Pa. (269) on 7 August 1959, and 13 were captured there on 1 August 1961.

Upstream Mortality

There was a large mortality of shad upstream near the spawning grounds about the end of the spawning period. In 1963, I observed many dead fish along the banks or in shallow water on 5 July; and a surface gill net set overnight at Milford, Pa. on 22 June captured 15 fish that appeared to have been dead for several days. In 1964, dead shad first appeared in the East Branch near Hancock about 14 June; on that date, I walked the bank for about 0.8 km and observed 26 dead fish within 10 m of the shoreline. I observed hundreds of dead shad on 8 July 1964 during a 19-km float from Matamoras, Pa. (274) to Dingmans Ferry, Pa. (258). I frequently saw dead fish in shallow water during August.

Shad may die before being completely spent. Some dead fish examined near Hancock had ovaries about a fourth the size of those in fish captured at Lambertville. The ovaries of these dead fish contained many translucent eggs, a criterion (Milner 1874; Brice 1898; Leach 1925) indicating that the fish is ripe.

Feeding Behavior in Fresh Water

Feeding did occur in freshwater, at least near the upstream spawning grounds. The stomachs of most shad captured at Lambertville were empty, but a few contained a slight amount of amorphous material. Stomachs of fish collected upstream from Port Jervis, N.Y. (295) in late May and June frequently contained a few insects. I observed a large mayfly hatch in late May 1964 near Hancock: hundreds of adult shad were rising to the surface, apparently to feed, and the stomachs of many fish (about 50) captured by angling were packed with mayflies. Similar surface feeding behavior was observed on several other occasions, although fish were not collected to confirm feeding. Many adults captured during the Tri-State Surveys contained recently eaten young shad and shield darters, *Percina peltata*. For example, four stomachs contained: 1) 2 darters and 9 young shad, 2) 6 darters and 17 shad, 3) 46 shad, and 4) 15 shad. Young shad were the first fish to react to rotenone, and the adults probably foraged on distressed and dying young.

Weight Loss in Fresh Water

Much weight was lost while the adult shad were in fresh water. Fish captured near Hancock had noticeably lost weight by late May, and they became more emaciated the longer they remained in fresh water. Tri-State Survey data obtained 10-13 July 1961 from Belvidere, N.J. (197) to Hancock, N.Y. and 16-17 July 1962 at Minisink Island and Skinners Falls were used to estimate the changed weight-length relationship for each sex. The relationships between total weight and length of these fish were $TW = 536.34 + 3.24(FL - 407.34)$ for 296 males and $TW = 661.29 + 3.01(FL - 451.18)$ for 19 females. Valid ranges for linear interpolation were about 265-450 mm for males and 340-475 mm for females. About 66% (males) and 63% (females) of the variation in total weight was associated with variation in length. These regressions explain less variation in total weight than the 80% explained for fish taken at Lambertville.

The average percentages of total weight loss in fresh water were estimated by comparing Lambertville and Tri-State Survey regression means at different lengths for each sex (Figure 1). The

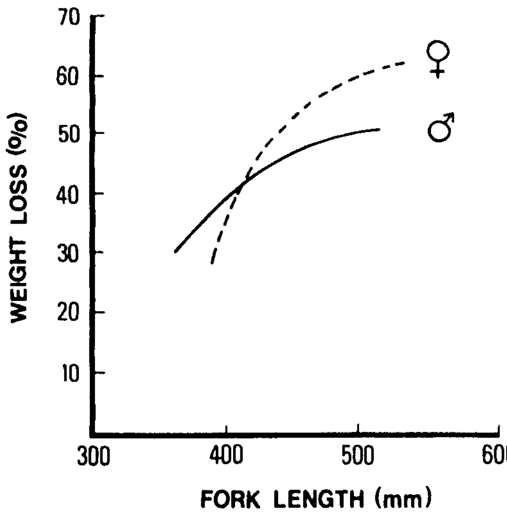

FIGURE 1.—Minimum average total weight loss of American shad in fresh water.

average percent weight loss depended upon length. Large fish lost a greater percentage than small fish. Average total weight loss was from 30 to 50% for 359-493 mm FL males and from 48 to 62% for 421-531 mm FL females, sizes which closely approximate the observed size range of fish in the 1963 and 1964 runs (Chittenden 1969). The observed mean fork lengths of fish captured at Lambertville were 428 mm for males and 477 mm for females, based upon the regression equations, and these sizes averaged 45 and 57% total weight loss, respectively.

Somatic weight loss, a better measure of the toll taken by the spawning migration, was estimated by subtracting the predicted total gonad weight from the predicted total weight at Lambertville before making a comparison with the Tri-State Survey total weight regressions. No correction was made for the gonads of fish captured during the Tri-State Surveys; however, these were a negligible fraction of the total weight. The total testes weights of 15 males collected near Hancock on 14 July 1964 and on 21, 24 June and 1 July 1965 ranged from 3.7 to 27 g and averaged 15.9 g while the total ovary weights of 3 females collected then varied from 18.2 to 35 g and averaged 27.1 g. The average percentage of somatic weight loss in males was 24% at 359 mm, 46% at 493 mm, and 42% for the mean-sized male of 428 mm. For females, somatic weight loss was 38% at 421 mm, 56% at 531 mm, and 50% for the mean-sized female of 477 mm.

Absolute daily weight loss was estimated from the duration of the freshwater residency. Fish captured during the Tri-State Surveys had probably been upstream about 75 days. This approximates their maximum stay in fresh water because the peak of the run at Lambertville is about 1 May (Chittenden 1969), and most fish move seaward from the Hancock area by late June. Therefore, the average daily loss in somatic weight of males was 1.63 g at 359 mm, 9.37 g at 493 mm, and 5.75 g for mean-sized males of 428 mm. For females the average daily loss in somatic weight was 5.75 g at 421 mm, 18.87 g at 531 mm, and 12.47 g for mean-sized females of 477 mm.

Daily weight loss can be used to suggest how long fish of different sizes can remain in freshwater before death. The amount of weight loss which results in death of shad is not known, but death occurs in many animals when weight loss exceeds 40% (Curtis 1949). Assume 50% for simplicity in calculation, this may not be quite correct, but it may be conservative and the size pattern, at least, remains the same if the percentage is a constant. From this, males could remain 154 days at 359 mm, 81 days at 493 mm, and the average sized male (428 mm) could remain 90 days. Females could remain 100 days at 421 mm but only 68 days at 531 mm, and the mean-sized female of 477 mm could remain 75 days. There is apparently little difference in the amount of time an average to maximum-sized fish can spend in fresh water before death, but small fish can survive much longer.

GENERAL DISCUSSION

Weight loss data presented herein agrees reasonably with those of Leggett (1972) who noted that his figures were probably underestimates. The present figures ignore weight loss in the 100-km migration between Marcus Hook and Lambertville and may be based on a longer than average stay in fresh water. Both factors tend to underestimate weight loss which affects related estimates.

Many shad apparently remain upstream near the spawning grounds well into the summer. However, the percentage they comprise of the run is unknown. A few fish remain far upstream until late fall. Bishop (1936) captured emaciated individuals 305-330 mm long near Hancock in November. These fish must have migrated upstream during the previous spring, because low dissolved oxygen water near Philadelphia presents a virtually impassable barrier through summer and fall (Ellis et al. 1947; Sykes and Lehman 1957; Chittenden 1969). Nichols (1959) captured an emaciated male during October in the Connecticut River and estimated it had been in freshwater at least 120 days. I captured an emaciated male (287 mm FL, 194 g) in fresh water in the James River, Va. on 7 October 1969.

The finding of little or no food in adults collected at Lambertville is similar to the reports of Bean (1903), Leim (1924), Leach (1925), Hildebrand and Schroeder (1928), Moss (1946), and Hildebrand (1963) that adults take little or no food while ascending rivers. My observations of instances of intensive feeding while upstream are exceptional, although Atkinson (1951) reported an artificial instance of feeding in freshwater ponds. Adult shad at sea feed largely on planktonic forms such as copepods and mysids (Leim 1924; Hildebrand and Schroeder 1928;

Bigelow and Schroeder 1953; Hildebrand 1963; Leim and Scott 1966), although Holland and Yelverton (1973) reported that they occasionally take large amounts of fish. Atkinson (1951) attributed the general absence of food in the stomachs of adults to their planktonic feeding habit and the absence of suitably large plankton in fresh water. My observations suggest that adult shad would opportunistically feed in fresh water if suitably large "planktonic" forms were readily available.

Although adults feed opportunistically in fresh water, they do not regularly obtain energy sufficient to maintain their weight and must use energy reserves accumulated during their life at sea to support migration in fresh water, final development of the gonads, and spawning. Adults use up their somatic substance at a size and sex dependent rate of at least about 1.6-18.9 g/day. Their physical activity deteriorates greatly as Fowler (1908) and Walburg (1960) noted. Death by starvation may occur when weight loss exceeds 40% (Curtis 1949), and this is probably the main cause of the mortality I observed on the spawning grounds. Further work is needed to quantitatively describe upstream mortality, but its magnitude would appear large as Bean (1892, 1903) and Anonymous (1902) also observed in the Delaware River and Walburg (1960) observed in the St. Johns River, Fla.

Weight loss was related to sex and size in agreement with Leggett (1972). The apparent relationship between weight loss and sex, however, may not be direct. Metabolic rate, in general, increases with temperature within limits. Leggett (1972) noted that females tend to migrate later and at a higher temperature than males and suggested that temperature was responsible for the apparent sex difference in weight loss. The relationship between size and total metabolism in a wide variety of organisms can be expressed as:

$$\log M = \log a + b \log W$$

where M is total metabolism and W is weight (Paloheimo and Dickie 1966; Prosser 1973). The relationship between metabolic rate and size can be expressed (Prosser 1973) as:

$$\log M/W = \log a + (b - 1) \log W.$$

From the latter expression it follows that a b value less than 1.0 implies that the metabolic rate decreases with increasing size, while a b value greater than 1.0 indicates that the metabolic rate increases with size. The value generally found for b is about 0.8 (Paloheimo and Dickie 1966; Prosser 1973), although Fry (1971) cautions that this value should not yet be accepted as dogma. Present findings on the relationship between size and weight loss in shad on their spawning migration are consistent with a b value greater than 1.0. Calculations made herein obviously assume that adult fish of all sizes are in fresh water the same length of time. If b is not greater than 1.0, we must conclude that: 1) small adults enter fresh water later than large fish and thus are in fresh water for a shorter period of time, or 2) small fish make better use of available freshwater food resources.

Estimates of the time that adults can remain in fresh water suggest that only small fish can survive upstream into the fall. The small fish I captured in the James River in October apparently had lost only about 33-39% of its weight in comparison with the Delaware River somatic weight regression at Lambertville and an unusually small fish (285 mm FL, 288 g) captured at Lambertville. It is noteworthy that, except for Nichols' (1959) report of a 430 mm FL male, the adult shad reported in fresh water during the fall have all been males about 305 mm long. Fish this small, however, are rare in the age compositions reported from many Atlantic Coast rivers (Talbot 1954; Fredin 1954; Walburg 1956, 1957, 1960, 1961; Sykes 1956; Sykes and Lehman 1957; Walburg and Sykes 1957; La Pointe 1958; Nichols and Tagatz 1960; Nichols and Massmann 1963; Godwin 1968; Leggett 1969; Chittenden 1975).

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