

**The Behavior of Adult American Shad (*Alosa sapidissima*)
During Migration from Salt to Fresh Water as Observed
by Ultrasonic Tracking Techniques**

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DODSON, J. J., W. C. LEGGETT, AND R. A. JONES. 1972. The behavior of adult American shad (*Alosa sapidissima*) during migration from salt to fresh water as observed by ultrasonic tracking techniques. *J. Fish. Res. Bd. Canada* 29: 1445-1449.

Five of seven adult American shad (*Alosa sapidissima*), tracked continuously with ultrasonic transmitters in the lower estuary of the Connecticut River in 1968 during their spawning migration to fresh water, exhibited extensive meandering, ranging 24-53 hr in duration in the region of the saltwater-freshwater interface. The salinity in the Connecticut River is like a wedge; its daily position is dependent on upland discharge, and its hourly position is dependent on tidal activity. The fish were observed during all tidal conditions and at several discharge rates, and in all cases they remained near the leading edge of salt water during the meandering phase. This behavior pattern was not a result of handling nor was it a typical behavioral response to tidal cycle. It was concluded that the meandering observed in the region of the saltwater-freshwater interface was due to physiological adaptation of the fish to fresh water. Of the remaining two shad tagged, one proceeded directly upstream without meandering, and one moved downstream.

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Des sept aloses savoureuses (*Alosa sapidissima*) suivies d'une façon continue à l'aide de transmetteurs ultrasoniques dans le bas estuaire de la rivière Connecticut en 1968 durant leur migration de fraie vers l'eau douce, cinq ont exécuté de vastes mouvements de va-et-vient, d'une durée de 24 à 53 h, à la limite entre l'eau salée et l'eau douce. La répartition de la salinité dans la rivière Connecticut est comme un coin, dont la position de jour en jour dépend du débit en provenance des hauteurs, et la position d'heure en heure dépend du balancement des marées. Les poissons, observés à tous les stades de marée et à plusieurs débits d'eau, demeurent, dans tous les cas, près du bord d'entrée de l'eau salée durant la phase de va-et-vient. Ce comportement n'est pas le résultat de la manipulation, non plus qu'une réaction typique au cycle de la marée. Nous en concluons que le mouvement de va-et-vient à la limite eau salée-eau douce est une conséquence de l'adaptation physiologique du poisson à l'eau douce. Des deux autres aloses marquées, une est entrée directement dans la rivière, sans va-et-vient, et l'autre s'est dirigée en aval.

Received January 13, 1972

This paper describes the behavior of adult American shad (*Alosa sapidissima*) in the lower estuary of the Connecticut River during that stage of the spawning migration associated with the transition from salt to fresh water.

Printed in Canada (J2400)

The Connecticut River is New England's largest river, discharging an average of 19,500 ft³/sec into Eastern Long Island Sound. Its mouth, constricted by a bedrock valley, is narrow. Because of its narrow mouth and large discharge, the salinity distribution in the lower river is a well defined "salt-wedge" (Meade 1966). This wedge consists of a narrow zone

located several miles upstream of the river mouth where Connecticut River water mixes with salt water. The salinity wedge moves up and downriver in accordance with tidal rhythm. Water on the river bottom may contain 15‰ chloride at high tide but be almost completely fresh in the same region at low tide. The position of the salinity wedge is also sensitive to changes in upland discharge. The salinity wedge is depressed downstream by increasing discharge. This also results in a steepening of the salinity gradient in both the horizontal (downriver) and vertical directions, the most saline end of the gradient being respectively downriver and on the bottom. Migrating adult shad enter the Connecticut River in April and May when river discharge varies 60,000–14,000 ft³/sec. At a discharge of 60,000 ft³/sec the salt wedge extends less than 1 mile upriver and, at a discharge of 14,000 ft³/sec, the salt wedge extends 6 miles upriver at high slack tide.

Materials and Methods

Seven adult shad were tagged internally with ultrasonic transmitters and tracked in the lower estuary of the Connecticut River during April and May, 1968. The sonic tags had a range of 100–2000 yards and an effective life of 2–3 weeks. Each tag was 2.5 inches in length, 0.5 inches in diameter, and weighed 0.5 oz in air. The receiving unit consisted of a portable battery-operated receiver tunable in the range 60KHZ–180KHZ, coupled to a hydrophone having a peak frequency of 70KHZ and a cone of reception of approximately 15°.

All fish were captured with 5½-inch (stretch measure) monofilament gillnets. Shad were removed from the net immediately upon capture and, if unharmed, were tagged by inserting a sonic tag into the stomach via the mouth. The fish were then gently returned to the water. Total time from capture to release was less than 1 min in all cases.

Fish were tracked continuously from an 18-ft outboard boat. The procedure involved maintaining the tracking boat in line with and directly behind the tagged fish, made possible by the directional characteristic of the hydrophone. The distance between fish and boat was estimated by changes in incoming signal strength. The position of the fish was obtained every 30 min by triangulation using navigational aids and prominent shore features as reference points. Fish position was plotted on enlargements of the navigation charts of the U.S. Coast and Geodetic survey. Tidal rate and direction were recorded coincident with each fish position.

No salinity observations were made in 1968 as no salinometer was available to us. To determine whether salinity was responsible for the observed movements, we predicted the salinity distribution in the lower estuary in 1968 using data obtained from the literature and salinity measurements made in the lower estuary in 1970 and 1971. Meade (1966) established that the position of the salinity wedge in the lower estuary of the Connecticut River is dependent on two major factors, upland dis-

charge and tidal conditions. Salinity measurements were taken at high and low slack water on several days in the spring of 1970 and 1971 to determine the upstream extent of the salinity wedge (salinity > 1‰). Daily discharge figures for 1970 and 1971 were obtained from the Thompsonville Gauging Station (located 70 miles upriver) of the U.S. Geological Survey, Water Resources Division. Discharge rates recorded at Thompsonville are followed a day later by equivalent changes in salinity at the mouth of the river (Meade 1966). The position of the upstream extent of the salinity wedge at high and low slack water was plotted together with the Thompsonville discharge reading for the previous day. Similar data obtained from Meade (1966) were also plotted, and curves were fitted to the points by eye (Fig. 1). Daily discharge values for 1968 were obtained from Thompsonville and the location of the upstream extent of the salinity wedge at high and low slack tide during the migrations of the tracked fish was read directly from Fig. 1 using the discharge rates for the day before the observations. The relation between the upstream position of the fish and the up-

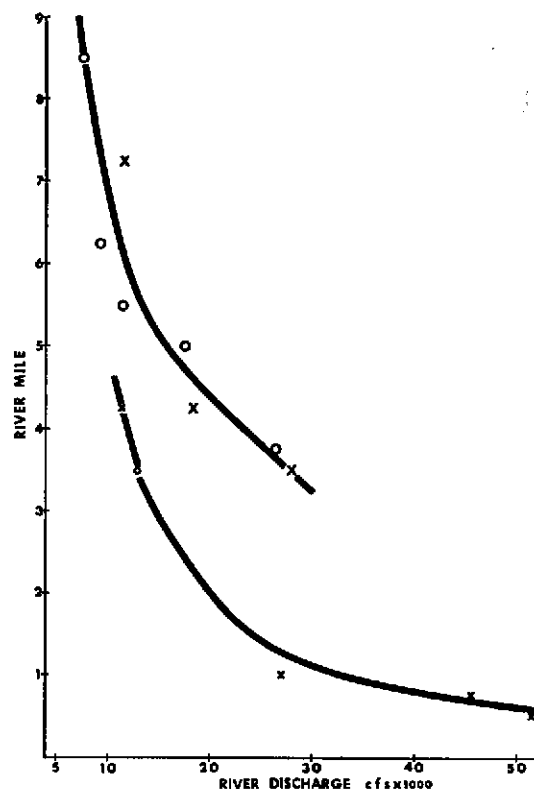


FIG. 1. Relation between river discharge, tide, and upstream extent of salt water in the lower estuary of the Connecticut River. The upper curve represents the leading edge of the salt wedge at high slack water. The lower curve represents the leading edge of the salt wedge at low slack water. X, points determined in this study (1970 and 1971); O, determined from Meade (1966).

stream position of the leading edge of the salinity wedge was examined by means of correlation analysis.

Comparisons were made between the behavior of migrating shad as revealed by this study and the behavior of shad migration exclusively in fresh water as revealed by the studies of Leggett and Jones (1967, 1968). The method and procedures used in both studies were similar.

Results

CHARACTERISTICS OF THE SALT WEDGE

The relation between discharge rates, tidal condition, and upstream extent of the salinity wedge in the lower estuary is illustrated in Fig. 1. The fish also experience a temperature change in passing from salt to fresh water. In early May, 1970, a 5 C increase in temperature coincided with reduction in salinity from 26‰ to 0‰. In mid-June of the same year, a 10 C increase in temperature coincided with reduction in salinity from 27‰ to 0‰. The observed increase in ΔT with time across the salinity wedge is due to a more rapid warming of river water relative to sea water.

Several other factors such as wind, deep holes, and islands affect the distribution of salinity in the lower estuary to a minor extent. These residual variations in salinity were not accounted for in our prediction of the upstream extent of the salinity wedge.

BEHAVIOR OF FISH

The behavior of five of the shad tracked in the lower estuary consisted of extensive meandering in the area of the upstream extent of salt water (Fig. 2). This movement resulted from a combination of passive drift and relatively inactive swimming. Leggett and Jones (in preparation) found the mean swimming speed of shad tracked in fresh water during 1967, 1968, and 1969 to be 2.1 ft/sec ($n=401$, $SD=1.3$). Dodson et al. (1970) found the mean swimming speed of shad tracked in Long Island Sound in salt water (28‰) during 1970 to be 2.5 ft/sec ($n=416$, $SD=1.4$) and during 1971 to be 2.4 ft/sec ($n=470$, $SD=1.2$) (Dodson et al. 1971). In comparison, the mean swimming speed for fish tracked in the lower estuary in this study was 1.3 ft/sec ($n=159$, $SD=.98$). This represents a significant reduction of swimming speed in the saline reaches of the river compared to both fresh ($P<.01$) and salt ($P<.01$) water. The fish were rarely observed to outswim the tide when oriented into it. Thus the fish were passively maintained near the leading edge of the salt wedge. Fish 1 was tagged 1.5 miles above the leading edge of the salt wedge and meandered for 53 hr (Fig. 2). During this interval the fish maintained itself close to the upper limit of the

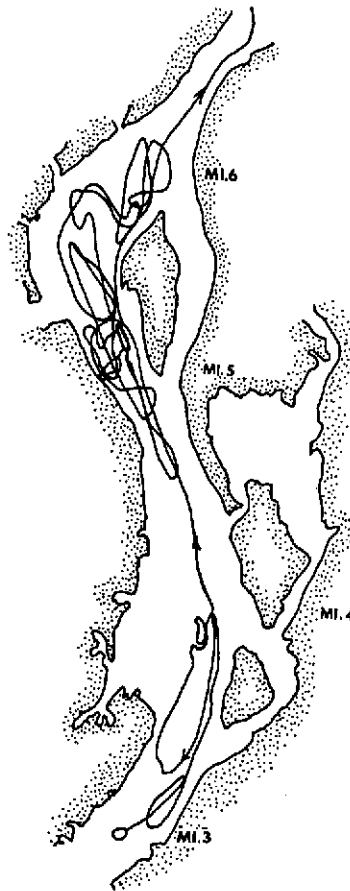


FIG. 2. The path of shad 1, tagged in the lower estuary of the Connecticut River at mile 3. This segment of the track lasted 45 hr. A further 8 hr of milling occurred in the vicinity of river mile 7 before continuous upstream migration occurred. See also Fig. 3A.

salt water wedge (Fig. 3A). Similar behavior was observed in four other shad. Fish 2 was captured at the leading edge of the salt wedge. After 37 hr meandering in the lower estuary (Fig. 3B), a direct upstream migration of 13 miles in 8 hr occurred. Fish 3 was captured 1½ miles below the upstream extent of salt water. The fish immediately migrated 3 miles upriver into fresh water where meandering behavior began and continued for 17 hr (Fig. 3C,1). Following this behavior, a direct upstream migration of 6 miles in 6 hr occurred. In all three cases, direct upstream migration occurred in fresh water and was continuous during periods of zero and reverse flow resulting from tidal action. Fish 4 (Fig. 3C,2) and Fish 5 (Fig. 3D) showed similar meandering behavior in the vicinity of the upstream extent of salt water but were lost before upstream migration occurred.

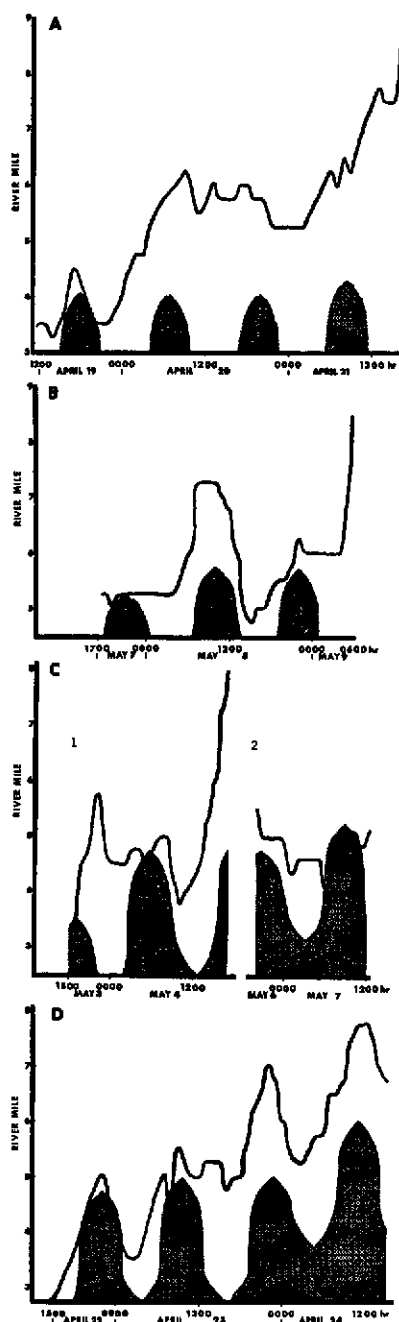


FIG. 3. A, The relation between the upstream displacement of shad 1 and the upstream extent of salt water at high and low slack water. The solid line represents the upstream displacement of the fish. Stippled area represents salt water. B, The relation between the upstream displacement of shad 2 and the upstream extent of salt water at high and low slack water. The solid line represents the

The subsequent upstream migration of these two fish was confirmed with data obtained from an automatic shore-based ultrasonic tag monitor located at river mile 7. Fish 4 moved upstream past the monitor at 1800 hr on May 9, 71 hr after tagging. Fish 5 moved upriver past the monitor for the final time at 0936 hr on April 25, 64 hr after tagging. The displacement of these 5 fish from the mouth of the river at the time of high and low slack water was positively correlated with the upstream extent of the salt wedge at these times ($r = .682$, $n = 27$, $P < .001$).

Of the remaining 2 shad, Fish 6 was tagged $1\frac{1}{2}$ miles above the leading edge of the salinity wedge and migrated 20 miles continuously upstream in 20 hr. Fish 7 was tagged 3 miles below the upstream extent of salt water and, after 10 hr of holding its position, it migrated downstream into Long Island Sound.

Discussion

The extensive meandering of 5 of 7 shad in the lower estuary could have resulted from three factors: (a) atypical behavior due to physiological shock resulting from handling; (b) normal behavioral response to the tidal cycle; or (c) behavioral response to the transition from salt to fresh water.

The observed meandering does not appear to be a result of handling. Fish 3 was tagged 1.5 miles below the leading edge of the salt wedge and migrated 3 miles upstream in 5 hr. Only then did it begin to meander in the vicinity of the upstream extent of the salt wedge. We would expect meandering to occur shortly after release if handling produced physiological shock. Leggett and Jones (1968) reported that 13 of 16 shad tagged in fresh water, and followed for more than 5 hr after tagging, resumed their upstream migration within 4 hr. In contrast, this study has shown that in the vicinity of the leading edge of the salinity wedge, meandering behavior of 5 of 7 fish exceeded 12 hr.

Similarly, meandering in the lower estuary does not appear to be a response to tidal cycle. Fish 1, 2, and 3 were tracked in the lower estuary and in fresh water. In each case, extensive meandering oc-

upstream displacement of the fish. Stippled area represents salt water. C, (1) and (2), The relation between the upstream displacement of shad 3 and shad 4 and the upstream extent of salt water at high and low slack water. The solid lines represent the upstream displacement of fish. Stippled area represents salt water. D, The relation between the upstream displacement of shad 5 and the upstream extent of salt water at high and low slack water. The solid line represents the upstream displacement of the fish. Stippled area represents salt water.

curred in the lower estuary whereas, in fresh water, upstream migration was continuous through conditions of zero and reverse flow due to tidal action. Leggett and Jones (1968) tracked two shad in fresh water within the tidal reach of the Connecticut River. Neither shad exhibited movement related to any stage of the tidal cycle. Similarly, 9 of 10 fish tracked in 1969 in fresh water showed no obvious changes in behavior related to tidal conditions (Leggett and Jones in preparation).

Two shad tracked in the lower estuary exhibited different behavior. Fish 7 returned to Long Island Sound after tagging. This fish was caught 3 miles below the leading edge of the salt wedge and may not have begun adaptation to fresh water at the time of capture. Fish 6 migrated upstream without hesitation.

We conclude that the observed meandering behavior of 5 of 7 shad tracked in the lower estuary of the Connecticut River is a consequence of the transition from salt to fresh water. The reactions of shad to specific salinities are not known as it is not possible to furnish accurate data on what salinity the fish were exposed to during the tracks. The prediction of the upstream extent of salt water is approximate and does not permit exact calculations of salinity values coincident with fish position. Furthermore, the position of the fish in the vertical salinity gradient is unknown as the ultrasonic tracking technique does not furnish information on fish depth.

Parry (1966), Milton (1971), and Bentley (1971) reviewed the literature on the physiological adaptations associated with the transition from salt to fresh water. Such a transition involves a number of changes in the osmotic composition of fish body fluid. The period of equilibration lasts for about 48 hr in eels and flounder transferred from fresh to salt water and 170 hr in steelhead trout (Bentley 1971). These times, however, represent the physiological equilibration period. No such data is available from the literature on the behavioral consequences of the transition from salt to fresh water or from fresh to salt water.

Tagatz (1961) showed that abrupt transfers of adult American shad from salt to fresh water caused some mortality where temperature was not a factor. Apparently shad must adapt slowly to fresh water. Those of our experimental fish tracked into fresh water meandered 24-53 hr at the leading edge of

salinity. Automatic monitor data extended the maximum milling time to 71 hr. These time differences may have resulted from differences in the stage of fresh water adaptation attained by each fish at the time of capture.

Acknowledgments

J. Carscadden, R. Galvin, and D. Ter Vrugt assisted in the tracking of shad. Dr D. Merriman, Director, and L. M. Thorpe, Associate Director of the Connecticut River Study, together with Drs J. W. Atz, M. R. Carriker, D. M. Pratt, E. C. Raney, and R. R. Whitney, scientific advisors to the Connecticut River Study, reviewed the manuscript. This project was funded in part with Anadromous Fish Act (PL. 89-304) funds through the U.S. Bureau of Commercial Fisheries, and with matching funds contributed by the Connecticut Department of Environment Protection and Connecticut Yankee Atomic Power Company.

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