Behavior of Adult American Shad (*Alosa sapidissima*) Homing to the Connecticut River from Long Island Sound

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The migratory behavior of American shad (*Alosa sapidissima*) approaching their natal river during the final saltwater stage of the spawning migration was studied using ultrasonic tracking and conventional tagging procedures. Initial displacement of most sonic-tagged shad released without displacement adjacent to and 10 km west of the Connecticut River was not in the direction of the home river. These fish, however, homed successfully to the Connecticut River as did dart-tagged shad released in the same areas.

Shad exhibited two major behavior patterns; countercurrent orientation in response to the reversing tidal current and adjustment of swimming speed to changes in tidal velocity. Countercurrent orientation was equally significant during daylight and darkness, whereas the adjustment of swimming speeds to tidal current velocity was more significant during daylight than darkness.

Shad tracked to the west exhibited a westerly bias inherent in the basic open water behavior patterns. Shad exhibited a greater degree of directed movement when oriented against the ebb tide and adjusted their swimming speeds to exceed the ebb tide velocity and to approximately equal the flood tide velocity. Shad tracked to the east exhibited the same major behavior patterns but with the opposite directional bias.

A hypothesis is presented suggesting that the location of the home river is achieved by means of a nonrandom search. Environmental clues indicative of the Connecticut River act to establish a preferred direction of displacement while the actual unidirectional displacement is achieved by reference to the rate and direction of tidal currents.

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Les auteurs ont étudié le comportement d'aloses savoureuses (*Alosa sapidissima*) au moment où elles s'approchent de leur rivière natale dans la phase finale en mer de leur migration de fraie. Ils ont fait appel au dépistage aux ultrasons et aux marquages ordinaires.

Le déplacement initial de la majorité des aloses munies de marques sonores et relâchées à l'endroit de capture à 10 km à l'ouest de la rivière Connecticut ne s'est pas produit en direction de la rivière natale. Ces poissons ont cependant réussi à revenir à la rivière Connecticut, tout comme des aloses marquées avec des dards et relâchées aux mêmes endroits.

Les aloses manifestent deux types principaux de comportement: une orientation à contre-courant en réponse aux changements de direction des courants de marée et réglage de la vitesse de nage en fonction des changements de vitesse de ce courant. Cette orientation à contre-courant se produit à la lumière du jour aussi bien qu'à l'obscurité, alors que le réglage de la vitesse natatoire par rapport à la vitesse du courant de marée est plus prononcé à la lumière du jour qu'à l'obscurité.

Les aloses suivies vers l'ouest montrent un biais marqué vers l'ouest qui est inhérent au comportement de base en pleine eau. Les aloses ont un mouvement dirigé de façon plus précise lorsqu'elles sont orientées contre le reflux et elles règlent leur nage à une vitesse dépassant celle du reflux et à peu près égale à celle du flux. Les aloses suivies à l'est se comportent généralement de la même façon mais avec biais en direction opposée.

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AMERICAN shad (*Alosa sapidissima*) undertake long distance oceanic migrations (Talbot and Sykes 1958; Sykes and Talbot 1958) and return to their home rivers to spawn (Walburg and Nichols 1967). Leggett and Whitney (1972) demonstrated that the timing and pattern of these extensive migrations are regulated by adherence to specific water temperatures in the range of 13–18 C. Seasonal changes in the 13–18 C isotherm along the Atlantic coast coincides with the southward migration of shad in the winter and the northward migration in the early spring and summer. The northward migration brings shad to the vicinity of their home rivers at times when river conditions are approaching the optimum for spawning.

Tagging studies also indicate that shad return to their natal streams to spawn (Truitt 1940; Hollis 1948; Vladykov 1950; Talbot and Sykes 1958; Nichols 1961). Leggett and Whitney (1972) reported that between 1965 and 1969, 18,374 mature shad were marked and released in the lower Connecticut River. Over 300 shad were recovered in the Connecticut River one year or more after tagging while none were recovered in other rivers.

Although the overall timing, route, and control mechanism of the shad migration is now established, the means by which shad locate and recognize specific natal rivers was heretofore unknown. This paper describes the behavior of adult shad, native to the Connecticut River, during their approach to the river from Long Island Sound and comments on possible environmental factors controlling the behavior.

Materials and Methods

The orientation and migratory behavior of shad was investigated by a combination of conventional tagging and ultrasonic tracking techniques. Conventional tags were used to assess the frequency of return of shad to the Connecticut River and the time taken to home. Ultrasonic tracking techniques (Trefethen 1956; Stasko, 1971) were used to analyze the minute to minute behavior of shad in response to various environmental variables.

ULTRASONIC TRACKING PROCEDURES

A total of 43 adult American shad fitted with sonic transmitters were tracked in Long Island Sound (Fig. 1) during April, May, and June of 1970 and 1971. The tags (Smith-Root model 69-B) had a frequency of 70 KHZ, a range of 30–300 m, depending on water conditions, and an effective life of 15 days. They were housed in polystyrene cylinders 6.4 cm long and 1.3 cm in diameter; approximate weight was 14.5 g in air. The receiving unit consisted of a portable battery operated receiver (Smith-Root model TA-60) tunable in the range 60–180 KHZ coupled to a hydrophone having a peak frequency of 70 KHZ and a cone of reception of approximately 15°. Swimming depth of tracked fish was unknown.

All fish were captured with 14-cm (stretch measure) monofilament gillnets and removed from the net immediately upon capture, as indicated by the movement of the headrope floats. If unharmed, a sonic tag was inserted into the stomach via the mouth and each fish was gently returned to the water.

Tagging was accomplished in two areas of Long Island Sound; (a) Westbrook, Connecticut (72°28′, 41°16′) and, (b) the west side of the Saybrook Point breakwater (72°20′40″, 41°15′50″) (Fig. 1). A third fishing area, located 10 km east of the Connecticut River, was fished in 1971. No shad were ever captured in this area.

Movements of these tagged fish were monitored by immediate and continuous tracking from a 6.4-m boat which was maintained behind and in line with the tagged fish. This was possible due to the directivity of the hydrophone which was manually rotated in the water. The distance between the fish and the boat was estimated by changes in incoming signal strength. The position of the fish was obtained at least every 30 min by triangulation. Whenever possible, cloud cover, wind strength and direction, wave condition, tidal condition, depth, temperature and salinity (measured at 2-m increments), and fish swim-speed (expressed as boat speed through the water) were recorded coincident with fish position. Temperature and salinity were measured with a Hydrolab TC-2 conductivity meter. Boat speed through the water was measured with a Gurly flowmeter.

Automatic shore monitors were utilized to detect the upriver passage of sonic-tagged shad which had previously been tracked at sea. In 1970, five shore-based monitors were located along the Connecticut River at points 7, 13, 31, 33, and 34 km upstream of the river's mouth. In 1971, two shore-based monitors were located 7 km upstream of the river's mouth. Each monitor contained two receivers which were connected to two hydrophones placed on the river bottom. The incoming signals to each receiver were recorded on separate tracks of a magnetic tape recording system. A time signal was automatically recorded on a third track every 6 min. The time of fish passage was obtained by adding the time marks in tenths of hours to the starting time of the tape. Individual fish were identified by the tag pulse, which was determined for each tag and recorded for each fish at the time of tagging.

The displacement of shad in Long Island Sound resulted from two factors: the speed and direction of tidal currents, and the heading and swimming speed of the fish. Data on tidal rate and direction were available from our records, and from tidal tables and charts for Long Island Sound. These data were combined and used together with observations of fish displacement over time to calculate fish bearing and swimming speed using triangulation and vector velocity techniques. Swimming speeds so calculated are hereafter referred to as "calculated swim-speeds." This represents the minimum speed at which a given fish must swim to travel a straight line between two points in a given increment of time. As such, it tends to underestimate the actual swimming speed, since straight line courses were seldom followed.

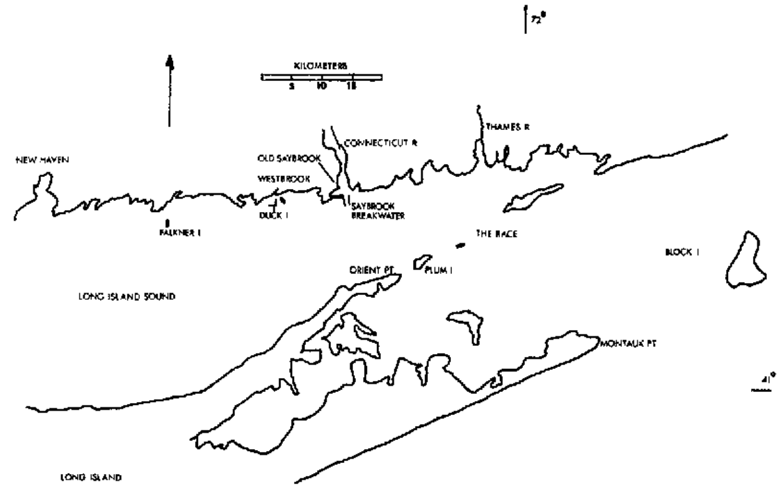

FIG. 1. Location map of Long Island Sound.

Current velocity values presented in the tidal charts and tables for Long Island Sound were obtained from measurements made to a maximum depth of 6 m (U.S. Coast and Geodetic Survey). As the depth of tracked shad could not be measured, a knowledge of differences in current velocity throughout the water column was necessary to assess the accuracy of swimming speed estimates. Riley (1956) reported that at midtide, when current velocities are maximum, the flood (westerly flowing) tide velocity remains relatively constant throughout the water column, whereas the ebb (easterly flowing) tide velocity is greater on the surface than on the bottom (30 m). Thus, the absolute magnitudes of swimming speeds calculated during ebb tide conditions may be overestimated if the fish were swimming deeper than 6 m. As the majority of shad were tracked within the 9-m contour line, we do not feel that this is a major source of error. Nevertheless, to avoid incorporating this possible source of error, swimming speeds calculated under each tidal condition were not directly compared. Rather, swimming speeds were examined relative to tidal velocity.

Swimming speeds were also estimated by recording the average speed of the boat through the water as the fish proceeded from one point to the next along the track. These estimates were biased as it was impossible to accurately integrate the observations over the entire $\frac{1}{2}$-hr period. They therefore tend to represent the swim-speed of the fish at the times of positioning and data collection rather than an average value between two points. These swim-speeds are hereafter referred to as "observed swim-speeds."

Conventional Tagging Procedures

Coincident with the sonic tracking experiments, a total of 330 shad were externally marked with nylon dart-type tags in 1970 and 1971 and released in the same areas as the sonic tagged shad. The numbers of fish recaptured in the Connecticut River by commercial and sport fishermen were analyzed for the frequency of return.

Analysis of dart-tag recoveries in the Connecticut River provided estimates of mean homing times from Westbrook and Saybrook. Dart-tagged shad were captured by sport and commercial fishermen from Old Saybrook at the river's mouth to Enfield Dam which is located 137 km upstream. Mean homing times were calculated by subtracting the time spent in the river from the total time elapsed between the tagging and subsequent recapture of shad. The time spent in the river was based on an estimated upstream migration rate of 6.1 km/day (Glebe and Leggett 1973).

Results

Paths of Migration and Homing Ability

Forty-three sonic-tagged shad were continuously tracked in Long Island Sound during 1970 and 1971 for a total tracking time of 613 hr. No shad were tracked into the Connecticut River. Furthermore, 40 of 43 shad exhibited a westerly displacement away from the Connecticut River (Fig. 2, 3). However, 7 (39.8%) of 18 dart-tagged shad released at Westbrook in 1970 were recovered in the Connecticut River by commercial fishermen during the same year. This recovery did not differ significantly from the recovery of 879 (21.8%) of 4072 dart-tagged shad released in the lower Connecticut River and subsequently recovered in the river during 1970 (Leggett 1970) (chi-square = 1.78, df = 1, $P > 0.5$). Similarly, 58 (18.6%) of 312 dart-tagged shad released in Long Island Sound in 1971 were recovered in the Connecticut River. This recovery did not differ significantly from the recovery of 864 (20.8%) of 4147 dart-tagged shad released in the lower Connecticut River and subsequently recovered in the river in 1971 (Leggett 1971) (chi-square = .59, df = 1, $P > .05$). These findings indicated that shad tagged at Westbrook and Saybrook were homing to the Connecticut River.

In 1970, 4 sonic tags were recovered by commercial and sport fishermen in the Connecticut River. The automatic shore-based monitors were plagued

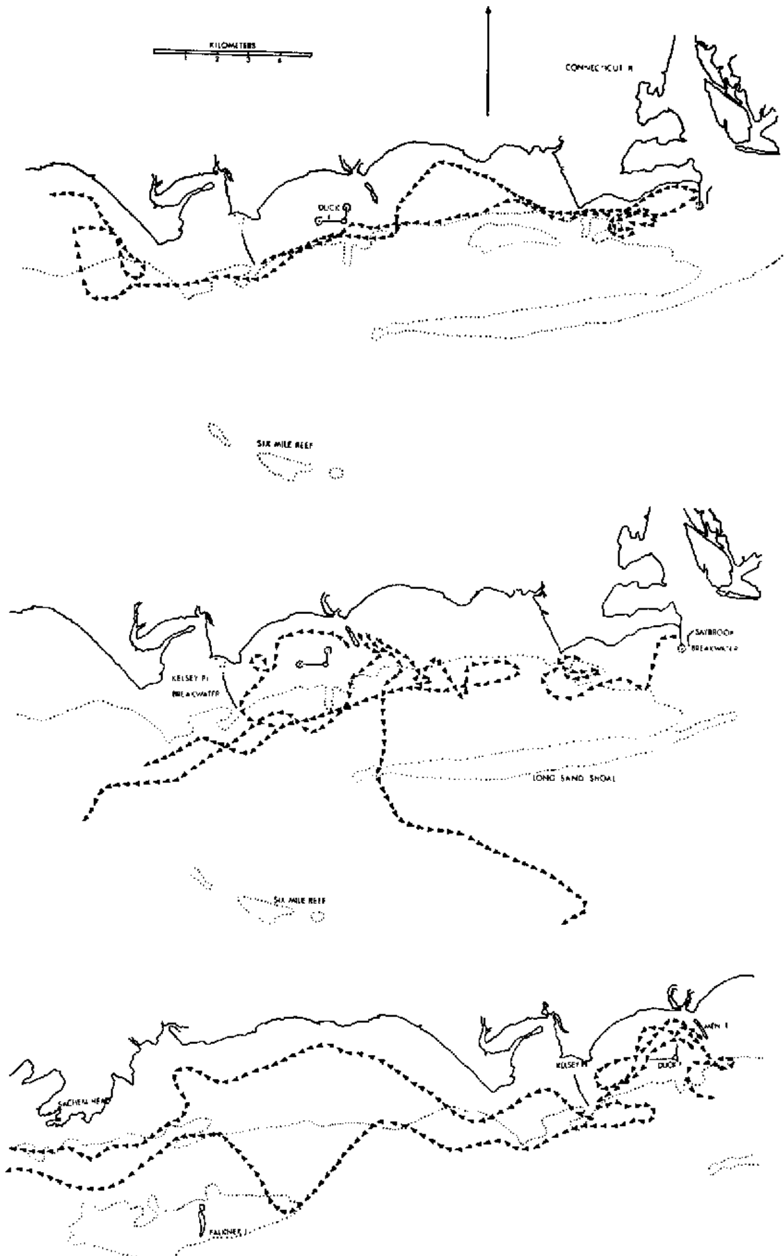

FIG. 2. Migration routes of 10 shad tracked in 1970. These shad were selected as being characteristic of the other tracks. Solid line represents shoreline, dotted line represents 9 m contour line, arrows represent direction of fish displacement.

by repeated malfunction in spite of daily inspection and testing. Interrogation of the magnetic tapes revealed 11 sonic tags recorded in 1970 and five in 1971. Tape advance malfunctions and time gaps in the monitoring system eliminated the possibility of identifying individual tags or their time of passage. However, it was possible to discriminate between different signals and thus to determine the minimum number of sonic-tagged shad entering the river.

Daily inspection of the monitors involved checking the tape advance mechanism, assessing the sensitivity of the hydrophones, and recording a short message on the tape for reference at the time of interroga-

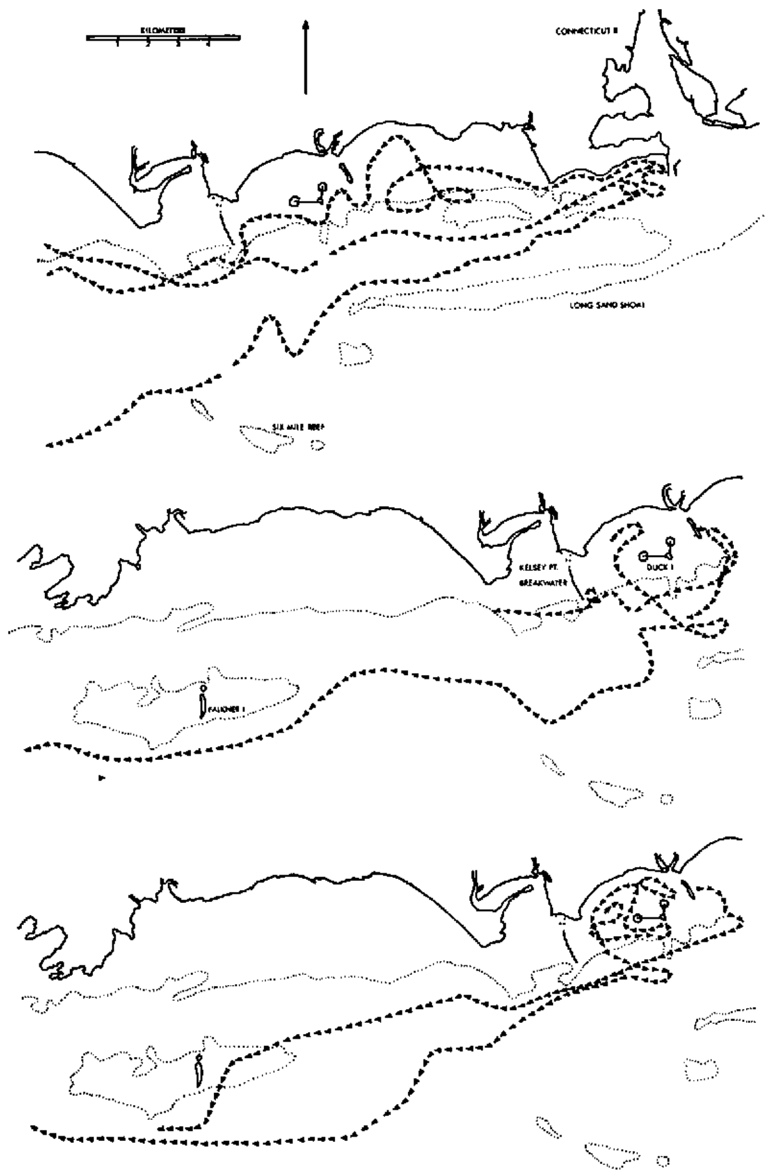

FIG. 3. Migration routes of eight shad tracked in 1971. These shad were selected as being characteristic of the other tracks. Solid line represents shoreline, dotted line represents 9 m contour line, arrows represent direction of fish displacement.

tion. Over 50% of these messages were not detected during tape interrogation indicating that the monitors also suffered malfunctions of the recording system. It was therefore impossible to estimate the monitors' efficiency of tag detection. The frequency of detection (37% or 16 of 43 sonic tags released) is believed to be compatible with the detection efficiency of the shore monitors and, therefore, indicative of successful homing to the Connecticut River.

The frequency of recovery of dart-tagged shad released at Westbrook in 1971 (23 of 106) was not significantly different from the frequency of recovery of dart-tagged shad released at Saybrook in 1971 (35 of 206) (chi-square = .69, df = 1, $P > .1$). The mean homing time for dart-tagged shad released at Westbrook in 1970 and 1971 was 7.9 days (SD = 6.7, $n = 25$), and for dart-tagged shad released at Saybrook was 5.2 days (SD = 4.9, $n = 20$).

These long mean homing times for fish migrating over relatively short distances indicated that the homing migration in Long Island Sound was extensive and not direct. This conclusion was supported by observations of the paths of shad tracked in 1970 and 1971 (Fig. 2 and 3).

In 1970, three shad were tracked east from Westbrook towards the Connecticut River. One shad turned west before arriving at the river, whereas the remaining two reached the river and remained in the vicinity of its mouth for approximately 2 hr before leaving. One was tracked west beyond Westbrook while the second migrated southeast (Fig. 4). No fish were tracked east in 1971.

Response to Tide

That portion of the data associated with open water migration, i.e. not associated with fish movements about breakwaters, islands, and similar obstructions, was extracted from the main body of data and analyzed. The 1st hr of individual tracks was excluded from the analysis to avoid incorporating nonsense behavior arising from possible temporary disorientation due to handling.

The data included 442 observations on 16 shad tracked in 1970 and 680 observations on 20 shad tracked in 1971. Seven shad were excluded from the analysis as they were either lost shortly after release or were tracked in areas where tidal current readings could not be obtained. Individual shad were analyzed if the shad were tracked through at least one tidal cycle. Twelve shad tracked in 1970 and 13 shad tracked in 1971 were analyzed individually.

Fish bearing — Long Island Sound is subjected to a reversing tide every 6 hr. The incoming (flood) tide flows approximately west and the outgoing (ebb) tide flows approximately east.

In 1970 and 1971, shad exhibited a strong tendency to orient into the tidal current.

1970, $r = -.479$, $n = 388$, $P < .001$, grouped data
1971, $r = -.502$, $n = 432$, $P < .001$, grouped data

This countercurrent orientation was equally significant during daylight and darkness. However, the precision of the countercurrent orientation differed depending on the direction of the tidal current. The countercurrent orientation of 9 of 12 shad tracked in 1970 was more precise when bearing west against the ebb tide (Fig. 5A). The remaining three shad exhibited greater precision when oriented to the east. Of these three, two (no. 07 and 08) initially pursued an easterly course towards the Connecticut River. Four shad, although exhibiting precise countercurrent orientation when bearing west, exhibited concurrent behavior under the influence of the westerly flowing tide. In 1971, the countercurrent orientation of 12 of 13 shad was more precise when bearing west into the ebb tide (Fig. 5B). The remaining shad exhibited similar precision during both tides. Four shad tracked in 1971 exhibited concurrent orientation under the influence of the flood tide. Three other shad approached this situation.

The differences in precision of countercurrent orientation between the two tidal conditions was also evident in the magnitude of angular changes in bearing exhibited by shad. Turning angles were smallest when shad were bearing west against the ebb tide. In 1970, the frequency of angular changes greater than 45° exhibited by shad tracked during ebb tide conditions was 33.3% (65 of 195 observations). The corresponding frequency during flood tide conditions was 57.3% (82 of 143 observations). This difference is statistically significant (chi-square = 7.48, $P < .01$). Similarly in 1971, the frequency of angular changes greater than 45° observed during ebb tide conditions was 24.7% (46 of 186 observations) and during flood tide conditions was 52.8% (104 of 197 observations). Again this difference is statistically significant (chi-square = 14.05, df = 1, $P < .01$).

Nineteen of 25 fish tracked in 1970 and 1971 and analyzed individually exhibited smaller turning angles when bearing west during ebb tide conditions (Fig. 6A–F). Six shad exhibited smaller turning angles when bearing east during flood tide conditions (Fig. 6G–I). Of these shad, three were initially tracked east to the mouth of the Connecticut River.

Angular changes in bearing exhibited by shad were not dependent on the time of day or the availability of celestial clues. There was no difference in the frequency of large turning angles (>45°) observed during day and night tracks (Table 1A). Similarly, the frequency of large turning angles did not differ between clear and overcast daytime

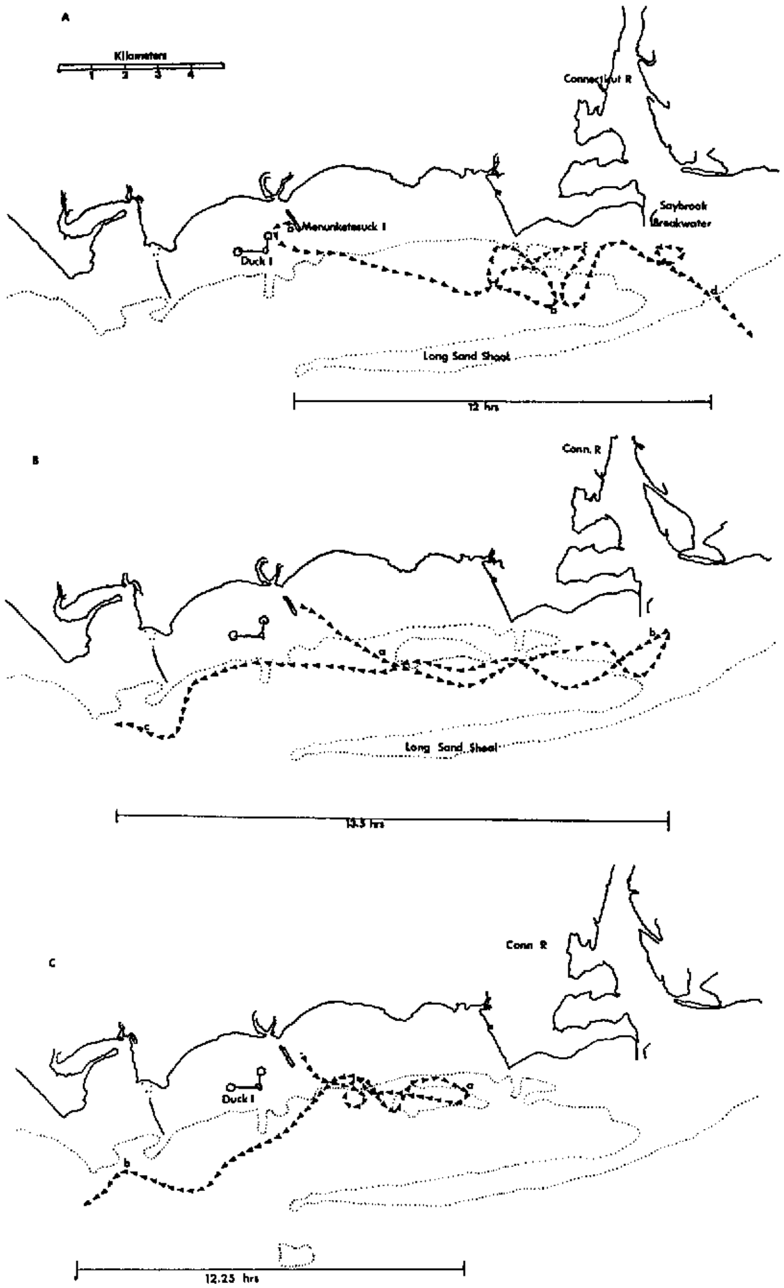

FIG. 4. Migration routes of shad initially tracked east to the Connecticut River. A, Fish no. 07. a–b, flood tide, b–c, ebb tide, c–d, flood tide; B, Fish no. 13. a–b, ebb tide, b–c, flood tide; C, Fish no. 08. a–b, flood tide.
Solid line represents shoreline, dotted line represents 9 m contour line, arrows represent direction of fish displacement.

skies (Table 1B) or between clear and overcast night skies (Table 1C).

Fish swimming speed — The mean calculated swim-speed of shad tracked in 1970 was 75.3 cm/sec (SD = 42.7) and in 1971 was 71.9 cm/sec (SD = 36.6). The frequency distribution of calculated swim-speeds for 1970 and 1971 are presented in Fig. 7. No diel periodicity was evident in shad swimming speeds.

A strong positive correlation was revealed between swim-speed and tidal current velocity in both 1970 and 1971. The correlation was more significant during daylight than darkness (Table 2). Analysis of 25 individual shad revealed that eight shad exhibited a significant adjustment of swim-speed to tidal velocity, five shad approached significance and 20 shad exhibited a positive relationship between swimming speeds and tidal current velocity.

The adjustment of swim-speed to tidal velocity differed according to tidal condition. Linear regression analysis of swim-speed/tidal velocity data revealed that in 1970, under ebb tide conditions, $b = 0.64$, and under flood tide conditions, $b = 0.25$. Thus, increment increases in ebb tide velocity produced greater increases in swim-speed than did similar increases in the flood tide velocity. In 1971, linear regression analysis revealed that, under ebb

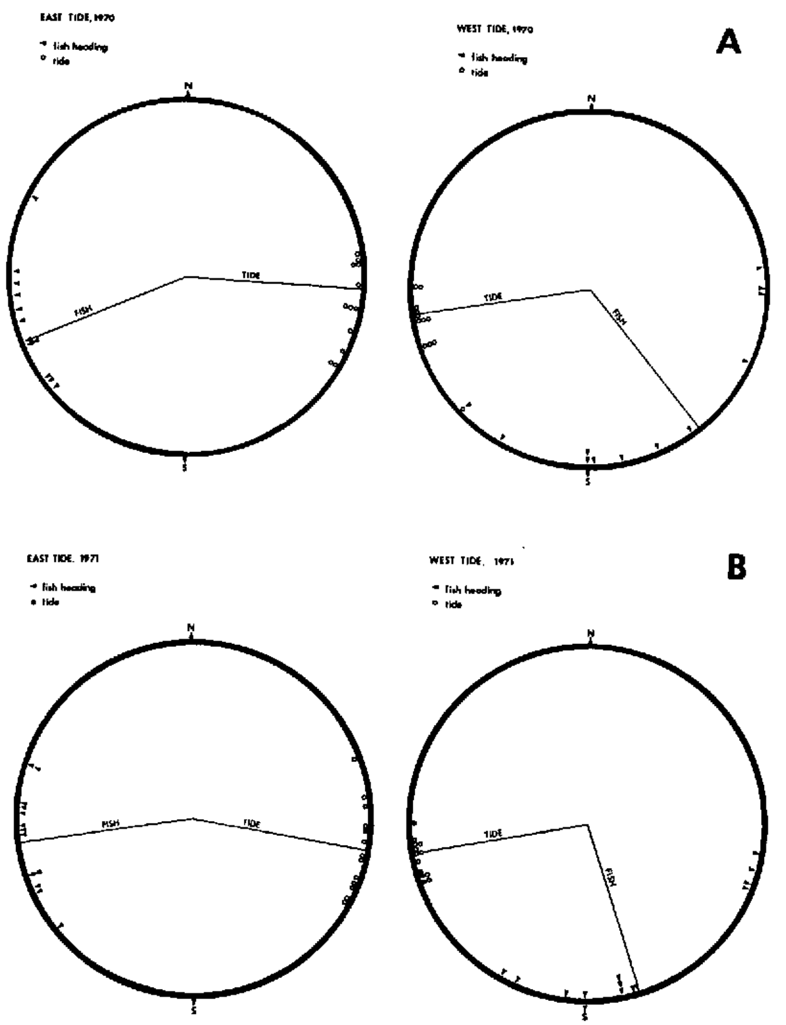

FIG. 5. Individual mean fish bearing and tide direction for shad tracked in 1970 and 1971.

tide conditions, $b = 0.45$. The regression was not significant for flood tide conditions.

In 1970 and 1971, shad swam west at a rate significantly greater than the ebb tide velocity (t-test, $P < .001$, grouped data) but under flood tide conditions swam at a rate approximately equal to the tidal velocity (Table 3). This relationship was observed during daylight and darkness (Table 4).

A sign test (Siegal 1956) applied to the swim-speed/tidal velocity data for individual shad tracked in 1970 and 1971 revealed that the majority of individual shad (22 of 25) swam at speeds in excess of the current velocity during ebb tide conditions ($P < .01$). Under flood tide conditions, the proportion of shad swimming at speeds in excess of tidal velocity (11 of 25) did not exceed the proportion swimming at speeds less than tidal velocity ($P < .4$).

Response to Temperature and Salinity

Decreased surface salinity and increased surface water temperatures in Long Island Sound are indicative of the presence of Connecticut River water. The results of a correlation analysis carried out on observed swimming speeds, surface salinity, and surface temperature revealed that in 1970 and 1971, 13 of 17 shad exhibited a negative relationship between observed swimming speed and surface salinity. This proportion was significantly greater than the proportion of shad exhibiting a positive relationship (binomial test (Siegal 1956) $P = .025$).

In 1970 and 1971, 11 of 20 shad exhibited a positive relationship between observed swim-speed and surface temperature. This proportion was not significantly different from the proportion of shad exhibiting a negative relationship (binomial test, (Siegal 1956) $P = .412$).

Discussion

The observed westerly displacement of 40 of 43 shad captured west of the Connecticut River suggested that these fish entered Long Island Sound from the east and migrated beyond their home river. Stevenson (1899) stated that the majority of shad entered Long Island Sound through the Race (Fig. 1). He further stated that most of these shad migrat-

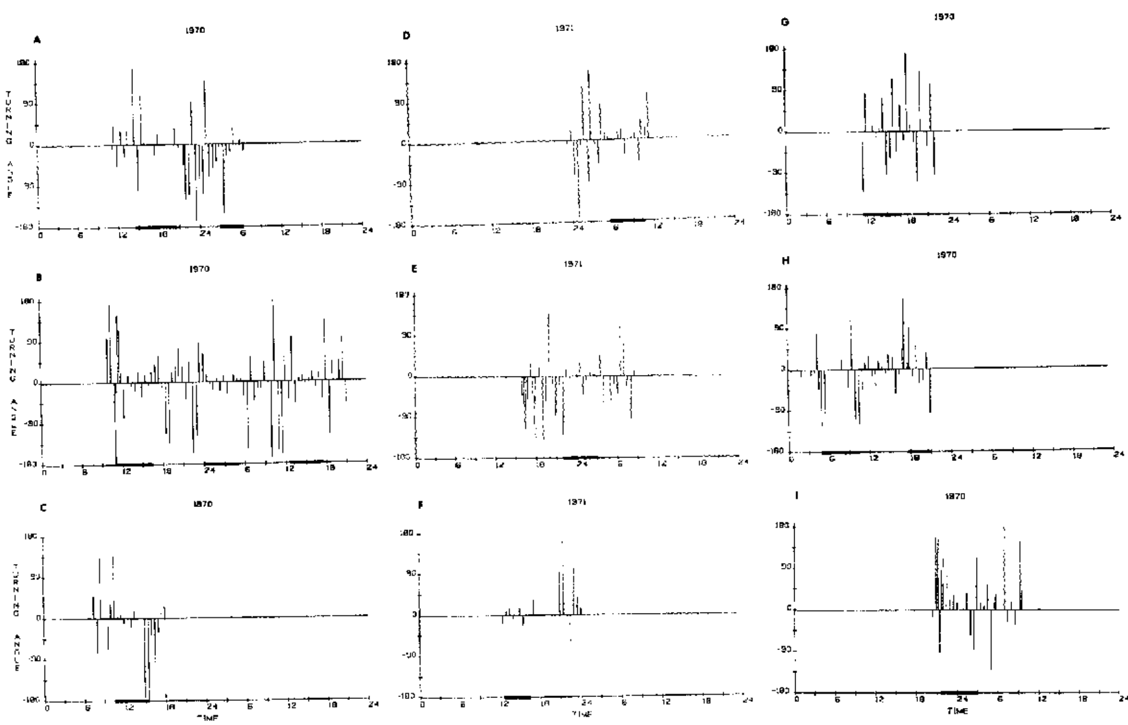

Fig. 6. Turning angles of six shad (A–F) initially tracked west in 1970 and 1971 and three shad (G–I) initially tracked east in 1970. A, Fish no. 02, 1970; B, Fish no. 06, 1970; C, Fish no. 03, 1970; D, Fish no. 12, 1971; E, Fish no. 08, 1971; F, Fish no. 13, 1971; G, Fish no. 08, 1970; H, Fish no. 07, 1970; I, Fish no. 13, 1970. Solid bar on the time axis represents duration of ebb tide (not including slack tide).

ed up the Connecticut River, but a large number proceeded westward to spawn in the Housatonic River and other smaller streams along the Connecticut shore. No shad were taken in the Housatonic River in 1960 and only occasional shad have been caught there since that time; dams and pollution have virtually eliminated this and other runs in rivers and streams located west of the Connecticut River (Walburg and Nichols 1967). In the light of this evidence and the recovery of dart- and sonic-tagged shad in the Connecticut River, it is concluded that shad caught west of the river were Connecticut River shad which had migrated beyond their natal river.

TABLE 1. Frequency of large turning angles exhibited by American shad (*Alosa sapidissima*) during (A) day and night, (B) clear and cloudy days, and (C) clear and cloudy nights in Long Island Sound.

	Year	*n*	%>45°	*n*	%>45°	Chi^2	*P*
		Day		*Night*			
(A)	1970	236	43.2	135	45.1	.05	>.05
	1971	260	36.2	149	42.3	.66	>.05
		Clear days		*Cloudy days*			
(B)	1970	124	45.2	112	41.1	.159	>.05
	1971	135	38.5	125	33.6	.319	>.05
		Clear nights		*Cloudy nights*			
(C)	1970	61	40.9	74	48.6	.301	>.05
	1971	91	43.9	58	39.7	.110	>.05

Historically, the most successful shad fishery in Connecticut was located west of the Connecticut River along the north shore of Long Island Sound. Three-pound nets located here caught more shad than all others combined (Walburg and Nichols 1967). In contrast, few shad have ever been caught east of the Connecticut River. A shad population native to the Thames River, located to the east of the Connecticut River (Fig. 1), was eliminated by 1896 (Stevenson 1899). Only a few shad have been caught in the Thames River since that time (Walburg and Nichols 1967). This evidence and our own failure to capture shad east of the Connecticut River leads to the conclusion that shad, native to the Connecticut River entering Long Island Sound via the Race, do not approach the northern shoreline at points east of the Connecticut River. Rather, the main body of Connecticut River shad appears to concentrate along the north shore of Long Island

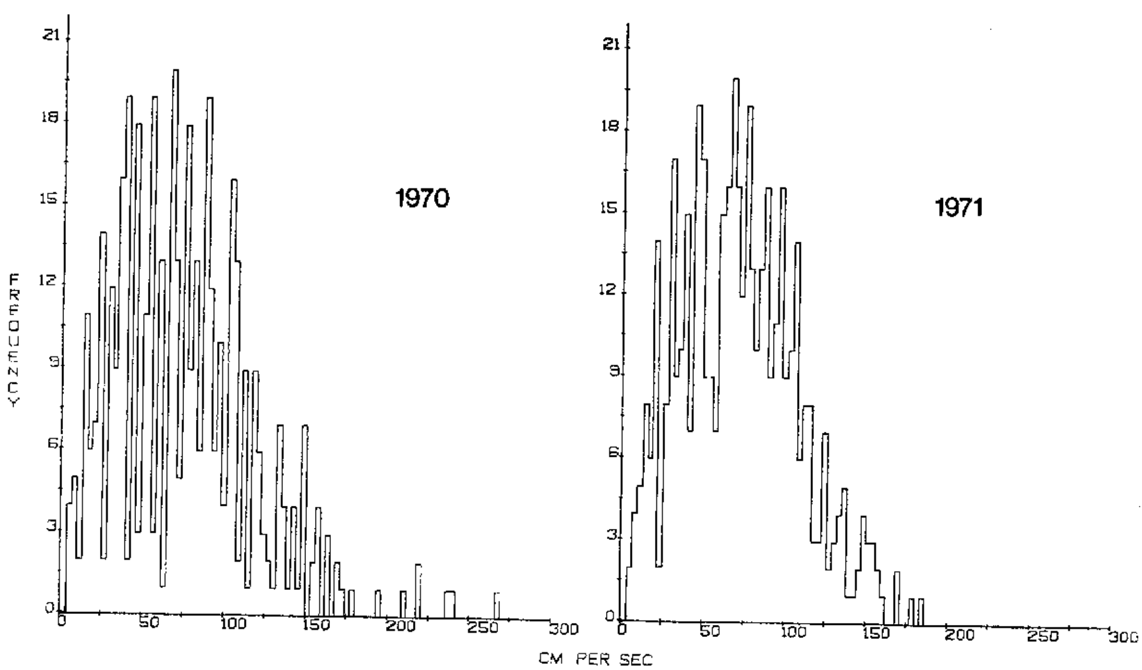

FIG. 7. Frequency distribution of calculated shad swimming speeds, 1970 and 1971.

Sound adjacent to and west of the Connecticut River prior to entry into the river.

Analysis of the behavior of shad tracked in Long Island Sound revealed a well-defined behavior pattern highly correlated to tidal conditions. Shad exhibited countercurrent orientation in response to the reversing tidal current, but the precision and directivity of the orientation was greater when bearing west against the ebb tide than during flood tide conditions. Shad adjusted their swimming speed to changes in tidal current velocity in a manner which resulted in swimming speeds in excess of the ebb tide velocity. Under flood tide conditions, swim-speeds were approximately equal to tidal current velocity. The result of this westerly bias inherent in the open water behavior pattern was a westerly displacement.

Analysis of individual shad revealed that during flood tide conditions, the behavior of shad varied from countercurrent orientation to concurrent orientation. Eight of 25 shad exhibited the latter tendency. Such behavior, however, also resulted in a westerly displacement in Long Island Sound.

To successfully home to the Connecticut River, shad tracked to the west must alter their behavior pattern to affect the opposite directional displacement. Three shad tracked to the east exhibited a partial alteration of the open water behavior pattern described for shad tracked to the west. Fish no. 07–70, 08–70, and 13–70 exhibited a lower frequency of large turning angles during flood tide conditions implying a greater degree of directed movement when bearing east. However, no directional bias was evident in the adjustment of swimming speed to tidal velocity. Fish no. 07 swam at speeds in excess of both tidal velocities, whereas fish no. 08 and 13 swam at speeds less than both tidal velocities. In spite of the limited number of observations on shad initially tracked east in Long Island Sound, the results indicated that shad tracked to the east and to the west exhibited the same major behavior components of countercurrent orientation and swim-speed adjustment to tidal velocity. Only the unidirectional bias inherent in these behavior components was altered to produce the initial easterly displacement. Thus, at least two orientation mechanisms are implicated in the migration. One is involved with orienting shad to tidal rate and direction, the other determines the directional bias inherent in the open water behavior pattern.

Several sensory modalities could be involved in governing the observed rheotaxic response of shad.

TABLE 2. Correlation analysis of calculated swim-speed vs. tidal current velocity in Long Island Sound, 1970, 1971.[a]

Year	Condition	N	*r*	*P*
1970	All	416	.313	$P<.01$
	Day	272	.349	$P<.001$
	Night	144	.257	$P<.01$
1971	All	470	.155	$P<.01$
	Day	288	.206	$P<.01$
	Night	182	.083	$P>.05$

[a]All figures cm/sec.

TABLE 3. Mean shad swim-speed and mean tidal velocity under ebb and flood tide conditions, 1970 and 1971.

	Westerly tide			Easterly tide		
	mean	SD	*n*	mean	SD	*n*
1970						
Tide	68.8	30.2	173	63.8	29.1	213
Fish	69.1	42.2	173	83.5	43.6	213
1971						
Tide	64.1	30.6	218	58.5	25.6	214
Fish	65.5	35.7	218	80.2	33.9	214

TABLE 4. Mean tidal velocity and mean shad swim speed during hours of daylight and darkness, 1970 and 1971. *P* — level of significance as determined by *t*-test.

	Westerly flowing tide						Easterly flowing tide					
	n	Tide vel	SD	Fish vel	SD	*P*	*n*	Tide vel	SD	Fish vel	SD	*P*
1970, Day	123	67.0	29.5	68.6	42.4	$>.05$	124	62.7	28.0	84.9	40.2	$<.01$
1970, Night	50	73.2	31.7	70.3	42.1	$>.05$	89	65.4	30.6	81.4	47.9	$<.01$
1971, Day	134	65.4	30.6	71.9	36.8	$>.05$	129	57.6	24.7	82.3	34.4	$<.01$
1971, Night	84	64.5	30.6	54.9	31.5	$<.05$	85	59.9	27.0	76.7	33.2	$<.01$

The countercurrent behavior observed in speckled trout (Elson 1939), salmon and eels (Davidson 1949), coho and chum salmon fry (Mackinnon and Hoar 1953) and cod, whiting, whiting-pout, smelt, and herring (Harden Jones 1963) appears to have been achieved through reference to optical stimuli. However, shad tracked in Long Island Sound exhibited countercurrent orientation at night as well as day and displayed similar frequencies of large turning angles under both conditions. Riley and Schurr (1959) observed extinction coefficients in Eastern Long Island Sound that varied from .39 to .82. High extinction coefficients were believed to be due to silt kept in suspension by strong, scouring tidal currents. Therefore, the maintenance of countercurrent orientation at night by optical stimuli would be possible only if shad were migrating very near the surface. Tactile stimuli may have been utilized if the fish were migrating close to the bottom.

The tendency of shad to orient in an easterly direction during flood tide conditions appears to be ill-adaptive for fish affecting a westerly displacement. This phenomenon, however, may be a basic behavior trait resulting from the oceanic migration. The northern migration of shad in the spring from North Carolina and Virginia is coastal (Talbot and Sykes 1958; Leggett and Whitney 1972). In inshore waters along the middle Atlantic states, the prevailing ocean current is southerly. This southerly flow extends well across the continental shelf during the spring and may attain velocities of up to 18 km/day (Bumpus and Lauzier 1965). Thus shad migrating north in the spring must maintain countercurrent orientation at all times to proceed northwards. Therefore, it appears that the behavior exhibited by shad in Long Island Sound is a continuation of a more basic behavior pattern with only the unidirectional bias inherent in the behavior being altered.

The partial breakdown of the ability of shad to adjust swimming speeds to changes in tidal current velocity during darkness suggested that optical clues may be involved in this response. Such clues would be removed or reduced during darkness. Shad, however, did not exhibit any speed reduction at night. Thus, shad did not display a diurnal rhythm of activity such as has been observed in chinook salmon in a river system (Johnson 1960) and sockeye salmon in a costal situation (Madison et al. 1972). Madison et al. observed a departure from the diel rhythm of swimming speeds characteristic of sockeye salmon when one fish was tracked into an inlet situation. They believed this may have been due, in part, to the bidirectional flow in the inlet. This is compatible with our observations of shad migrating in Long Island Sound which also exhibits a strong bidirectional flow.

Although the behavior of shad was most obviously related to tidal current rate and direction, these two variables in themselves are not indicative of the location of the Connecticut River. Therefore, other environmental variables, indicative of the Connecticut River, must be responsible for establishing the unidirectional bias inherent in the open water behavior pattern of shad. Celestial clues do not appear to play a role as shad behavior remained relatively constant throughout periods of clear and cloudy daytime and nighttime skies.

The observed tendency of shad to increase swimming speeds in response to lowered salinities suggested that water-borne chemical clues may play a role in the location of the natal river. During the shad spawning season of 1970 and 1971, the Connecticut River was responsible for 75–78% of the total freshwater inflow into Long Island Sound (Water Resources Division, United States Geological Survey, Hartford, Conn.). Furthermore, Connecticut River water has been detected off Montauk Pt. (Riley 1959), well within the proposed oceanic migration route of shad. Thus, shad migrating in areas of decreased salinity could obtain clues characteristic of the natal river. However, the freshwater plume discharged from the Connecticut River becomes fragmented and spread to the east and to the west of the river by the strong bidirectional current. As a result, the response of shad to lowered salinities cannot be defined in terms of orientation towards or away from the Connecticut River. Indeed, if shad do use chemical clues to establish a preferred direction of movement in Long Island Sound, the dispersal and dilution of Connecticut River water over much of northeastern Long Island Sound may be in part responsible for the initial migration of shad beyond their natal river. As shad proceed west, chemical clues indicative of the Connecticut River would become less evident and foreign chemical clues originating from other rivers would become more prevalent. This in turn may evoke the opposite directional bias.

Other clues may be responsible for the reversal in unidirectional displacement that must be affected by shad migrating west of the Connecticut River. The shallow and enclosed western portion of Long Island Sound is 3–5 C warmer than the eastern end (Riley 1959). West of the Connecticut River, spring freshening begins earlier and the more sluggish circulation patterns of the western end cause an approximate 5‰ reduction in the level of salinity relative to the eastern end (Riley 1959). The major east–west trench systems running from the deep waters of the eastern end to the shallow waters of the western end could also act as topographical reference points. Any or all of these clues could provide shad with orientational or positional information.

The location of the Connecticut River by shad migrating in Long Island Sound appears to depend to a large degree on an extensive but nonrandom search. This conclusion is based on the long period of time required by shad to home to the Connecticut River from points relatively close to the river mouth and the observed westerly displacement affected by Connecticut River shad already west of the river. We hypothesize that shad migrating along the eastern coast of North America in the vicinity of Long Island Sound detect clues indicative of the Connecticut River that establish a unidirectional bias resulting in a westerly movement towards the Connecticut River. If the river is not located on the first leg of the migration and shad proceed west of the river, some stimuli, presently unknown, evoke the opposite unidirectional bias resulting in an easterly displacement towards the Connecticut River. Under both conditions, the open water behavior pattern continues to be most directly oriented by the rate and direction of the tidal current, while the clues responsible for evoking the unidirectional bias cease to be orienting clues once the bias is established. This sequence may be repeated several times before the river is located.

The culmination of the behavior sequence exhibited by shad occurs on entry into the river. The results of this study have shown that proximity to the Connecticut River does not ensure entry into the river and, therefore, other factors must be involved. A temporal restriction related to the shad's state of receptiveness to certain environmental stimuli may be imposed upon the behavioral sequence described.

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