

Role of Olfaction and Vision in the Behavior of American Shad (*Alosa sapidissima*) Homing to the Connecticut River from Long Island Sound

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Twenty-two adult American shad (*Alosa sapidissima*), captured, sensory-impaired, sonic-tagged, and released adjacent to and 10 km west of the Connecticut River, were tracked in Long Island Sound in 1972. Both anosmic and blind/anosmic shad oriented into the tidal current and altered swimming speeds in relation to changes in tidal current velocity as do unimpaired fish. They did not, however, exhibit the consistency in these behavioral responses that resulted in westerly displacement in unimpaired shad. Blind shad exhibited neither of these behavior patterns but did tend to affect a westerly displacement in Long Island Sound.

Dart-tagged adult shad that were sensory-impaired and released without displacement in the same areas of Long Island Sound in 1971 and 1972 homed less successfully to the Connecticut River than did unimpaired dart-tagged shad released in the same years. Anosmic dart-tagged shad located the Connecticut River less successfully than unimpaired shad. Blind shad successfully located the river from 10 km distance but failed to do so when released adjacent to the river. Blind/anosmic shad failed to locate the river from either release site.

It was concluded that an olfactory-rheotactic mechanism forms the basis of the location of the Connecticut River by shad. The preferred direction of displacement appears to be established by olfactory clues indicative of the Connecticut River whereas the orientation along the migratory path is maintained by reference to the rate and direction of tidal currents. Vision alone cannot account for this rheotactic response.

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Vingt-deux aloses savoureuses (*Alosa sapidissima*) adultes, capturées, rendues aveugles et anosmiques, équipées de marques ultrasonores et relâchées à proximité et à 10 km de la rivière Connecticut, ont été suivies dans le détroit de Long Island en 1972. Les aloses anosmiques, de même que les aloses aveugles/anosmiques se sont orientées dans le courant de marée et ont modifié leur vitesse de nage en réponse aux changements de vitesse du courant, tout comme les poissons intacts. Leurs réponses ne furent toutefois pas aussi uniformes que celles qui ont amené les aloses intacts à se déplacer vers l'ouest. Les aloses aveugles ne montrèrent aucun de ces modes de comportement, mais eurent tendance à se déplacer vers l'ouest dans le détroit de Long Island.

Les aloses adultes marquées de dards, dont les sens avaient été altérés et qui avaient été relâchées sans déplacement dans les mêmes régions du détroit de Long Island en 1971 et 1972, eurent moins de succès à retourner à leur rivière d'origine, la rivière Connecticut, que les aloses intacts marquées de dards et relâchées ces mêmes années. Les aloses anos-

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miques marquées de dards eurent moins de succès à trouver la rivière Connecticut que les aloses intactes. Les aloses aveugles réussirent à localiser la rivière Connecticut d'une distance de 10 km, mais ne purent le faire lorsque libérées dans le voisinage de la rivière. Les aloses aveugles/anosmiques ne réussirent pas à localiser la rivière de l'un ou de l'autre site de remise à l'eau.

Nous en concluons qu'un mécanisme olfactif-rhéotactique permet à l'alse de localiser la rivière Connecticut. La direction préférée du déplacement semble être déterminée par des indices olfactifs conduisant à la rivière Connecticut, alors que l'orientation le long de la voie de migration est maintenue par référence à la vitesse et à la direction du courant de marée. La vision seule ne peut expliquer cette réponse rhéotactique.

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THE American shad (*Alosa sapidissima*), largest member of the herring family (Clupeidae), is native to the eastern coast of North America. It is anadromous, undertakes extensive oceanic migration, and returns to its natal river to spawn (Walburg and Nichols 1967). Dodson and Leggett (1973) demonstrated that adult shad native to the Connecticut River, and migrating in Long Island Sound during the final saltwater stages of the spawning migration, located their home river by means of an extensive nonrandom search. We hypothesized that environmental clues indicative of the Connecticut River acted to establish the westerly bias in the open water orientation of shad in Long Island Sound, while the actual displacement was achieved by adjusting swimming speeds and headings in response to changes in the rate and direction of tidal currents. This paper reports the results of studies designed to test this hypothesis and to identify the environmental clues instrumental in establishing and directing this behavior.

Materials and Methods

ULTRASONIC TRACKING

Twenty-two adult shad (45–55 cm) were tagged internally with ultrasonic transmitters, released without displacement, and tracked in Long Island Sound (Fig. 1) during April, May, and June, 1972. The tags had a pulsed output ranging from 60–200 pulses/min, a frequency of 70 kHz, a maximum range of 30–300 m, and an effective life of 15 days. They were housed in polystyrene cylinders 6.4 cm long and 1.3 cm in diameter; their weight in air was 14.5 g. The receiving unit was a portable 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 the tracked fish was unknown.

All fish were captured with 14-cm (stretch measure) monofilament gillnets. Capture was signalled by movement of the headrope floats and the fish were immediately removed by cutting the mesh holding the fish.

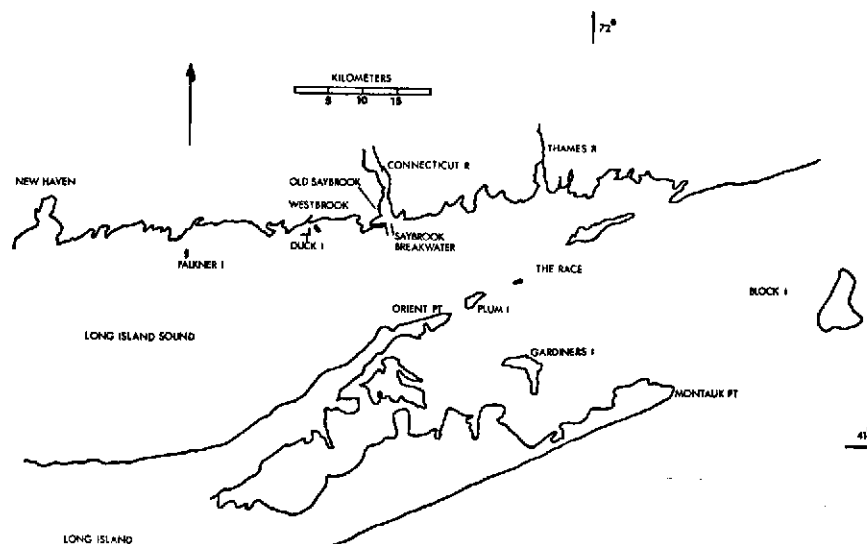


FIG. 1. Location map of Long Island Sound.

If the fish was undamaged by capture a sonic tag was inserted into the stomach via the mouth.

Seven shad were blinded by injection of 3% benzethonium chloride (Phemerol, Parke Davis and Co.) into the eyeball (McCleave 1967). Tests conducted in a live car anchored in salt water demonstrated that shad treated in this way lost sight within 1 h. Loss of sight was indicated by the eye turning white in color and by the increased frequency of fish colliding with the sides of the car. Eight shad were olfactory occluded by injection of silicone sealant (Dow Corning) into the nares. The sealant was sufficiently dense to block the entrance of water into the nares and had adequate viscosity to fill every fold of the nasal cavity. Shad heads treated in this way and left in violently running water for 48 h lost no plugs. On dissection, the plugs were observed to overlay the sensory epithelium completely. Seven shad were both blinded and olfactory occluded. Following insertion of the tag and sensory impairment, all fish were gently returned to the water without displacement. Total time from capture to release was less than 2 min in all cases.

Releases were made at two sites in Long Island Sound: a) Westbrook, (72°28', 41°16')—three blind shad, four olfactory occluded (anosmic) shad, three blind/anosmic shad; b) west side of the Saybrook breakwater (72°20', 41°15'50")—four blind shad, four anosmic shad, four blind/anosmic shad (Fig. 1).

Movements of sonic-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 manually rotated hydrophone. The distance between the fish and the boat was estimated by changes in incoming signal strength which was roughly calibrated for each tag prior to release. The position of the fish (accurate to within 50 m) was obtained at least every 30 min by triangulation using navigation aids and prominent shore features. When possible, cloud cover, wind strength and direction, wave condition, tidal condition, depth, temperature and salinity (measured at 2-m depth increments), and boat speed through the water were recorded coincident with fish position. Temperature and salinity were measured with a Hydro-lab TC-2 conductivity meter. Boat speed through the water was measured with a Gurly flowmeter.

The 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 first hour of individual tracks was excluded from the analysis to avoid incorporating nonsense behavior arising from possible temporary disorientation due to handling.

Long Island Sound experiences a reversing tidal current which floods to the west and ebbs to the east. The movement of sonic-tagged shad in Long Island Sound thus resulted from the combined effects of the rate and direction of the tidal current and the heading and swimming speed of the fish. Data on tidal rate and direction during the tracks 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 movement over time to calculate fish heading and swimming speed through the water using triangulation and vector velocity techniques. Swimming speeds determined in this way are referred to as "calculated swimming speeds" and represent the minimum speed at which a fish must swim to travel a straight line between two points in a given increment of time. This calculation tends to underestimate the actual swimming speed since straight line courses were seldom followed.

Current velocity values presented in the tidal charts and tables for Long Island Sound were derived from measurements made to a 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 calculations. Riley (1956) reported that at midtide, when current velocities are maximum, the velocity of the flood (westerly) tide remains relatively constant throughout the water column, whereas the ebb (easterly) tide velocity is greater at the surface than at the bottom (30 m). Thus swimming speeds calculated during ebb tide conditions may be overestimated if the fish were swimming deeper than 6 m. To avoid this possible source of error, swimming speeds calculated under different tidal conditions were not directly compared. Rather, swimming speeds were only analyzed relative to tidal velocity.

Swimming speeds were also estimated by observing the speed of the boat through the water as the fish moved from one point to the next along the track. These "observed swimming speeds" are also subject to some error since it was not possible to accurately integrate the range of the entire $\frac{1}{2}$ -h period of these speeds observed. They do, however, provide a reasonable approximation to average swimming speeds between successive positions along the track.

Arithmetic means were used to calculate mean fish headings during each tidal condition because the range of observed headings during each tidal cycle was less than 180°. Batschelet (1965) reported that such distribution can be considered linear and that under such conditions arithmetic means differ little from angular means. Mean headings were classified as countercurrent (fish heading $<45^\circ \pm$ reciprocal of tide heading), concurrent (fish heading $<45^\circ \pm$ tide heading), and crosscurrent (all headings other than those described).

Precision of unidirectional orientation under different conditions of tide and sensory impairment were analyzed by calculating the frequency of large turning angles ($>45^\circ$) observed under these conditions (Madison et al. 1972; Dodson and Leggett 1973).

All analyses were carried out on combined data from each impairment category. Individual tracks were similarly analyzed if the track duration extended through at least one full tidal cycle. The behavior of sensory-impaired shad observed in this study was compared with that of unimpaired shad tracked in 1970 and 1971 (Dodson and Leggett 1973).

CONVENTIONAL TAGGING

In 1971, 231 blind shad, 220 anosmic shad, and 312 unimpaired shad were externally marked with nylon dart tags and released without displacement from the same areas of Long Island Sound as the sonic-tagged shad. Olfactory occlusion was achieved by injecting the nares with vaseline and cotton plugs (Wisby and Hasler 1954). This procedure proved unsatisfactory and the data for dart-tagged anosmic shad released in 1971 were discarded. Blinding was effected by the method previously outlined for sonic-tagged shad.

In 1972, 141 blind shad, 143 anosmic shad, 128 blind/anosmic shad, and 150 unimpaired shad were dart-tagged and released at these sites. Olfactory occlusion of this group was by injection of silicone sealant into the nares as previously described.

Differences in the frequency of recovery of sensory-impaired and sensory-intact dart-tagged shad in the Connecticut River were used as a measure of the relative ability of the four groups to locate the river following release.

Results

CONVENTIONAL TAGGING

The frequencies of recovery, in the Connecticut River, of impaired and unimpaired dart-tagged shad are presented in Table 1. Blind and unimpaired shad released at Westbrook homed to the Connecticut River equally well from Westbrook. Blind shad released at Saybrook had a reduced homing success as compared with unimpaired shad. Anosmic shad were generally less successful than unimpaired shad in locating the river from both release areas. Three anosmic shad were captured far from the Connecticut River; one at Gardiner's Island and two at Montauk Point (Fig. 1). Blind/anosmic

shad failed completely to locate the Connecticut River.

The recovery frequency of unimpaired shad released in Long Island Sound in 1971 and 1972 did not differ significantly ($\chi^2 = 0.33, P > 0.1$). Furthermore, the recovery frequency of these shad did not differ significantly from the recovery of 8769 dart-tagged unimpaired shad released in the Connecticut River proper in 1971 and 1972 ($\chi^2 = 1.83, P > 0.1$).

The mean homing time of dart-tagged sensory-intact shad released at Westbrook in 1971 (7.9 days, $SD = 6.7, n = 25$) and in 1972 (7.6 days, $SD = 4.6, n = 6$) was not significantly different ($t = 0.10, P > 0.1$). Similarly, the mean homing time of dart-tagged sensory-intact shad released at Saybrook in 1971 (5.2 days, $SD = 4.9, n = 20$) and in 1972 (6.3 days, $SD = 6.3, n = 11$) was not significantly different ($t = 0.54, P > 0.1$).

ULTRASONIC TRACKING

Paths of migration — Six of eight anosmic shad were tracked continuously after release in Long Island Sound (Fig. 2). Of the two remaining, one was lost immediately due to equipment failure and one failed to move suggesting that either the tag was regurgitated or the fish died after release. Anosmic shad 2 and 4 moved to the west during both ebb and flood tides whereas anosmic shad 1 and 3 moved to the east during both tidal conditions. Anosmic shad 5 and 6 moved to the west during the flood tide and to the east during the ebb tide.

Five of seven blind shad were tracked continuously after release (Fig. 3). Two were lost immediately after release due to poor weather

TABLE 1. Frequency of recovery in the Connecticut River of impaired and unimpaired dart-tagged American shad (*Alosa sapidissima*) released in Long Island Sound in 1971 and 1972. Chi-square values obtained from comparisons of recovery frequencies of each category of impaired shad with that of unimpaired shad. 5% probability level = 3.84.

Release area	Fish treatment	1971		1972		Combined		χ^2
		no. released	no. recap.	no. released	no. recap.	no. released	no. recap.	
Saybrook	Unimpaired	206	35	115	17	321	52	
	Blind	166	11	109	6	275	17	14.52
	Anosmic	—	—	111	10	111	10	3.47
	Blind/anosmic	—	—	97	0	97	0	×
Westbrook	Unimpaired	106	23	35	7	141	30	
	Blind	65	11	32	6	97	17	.61
	Anosmic	—	—	32	3	32	3	2.39
	Blind/anosmic	—	—	31	0	31	0	×

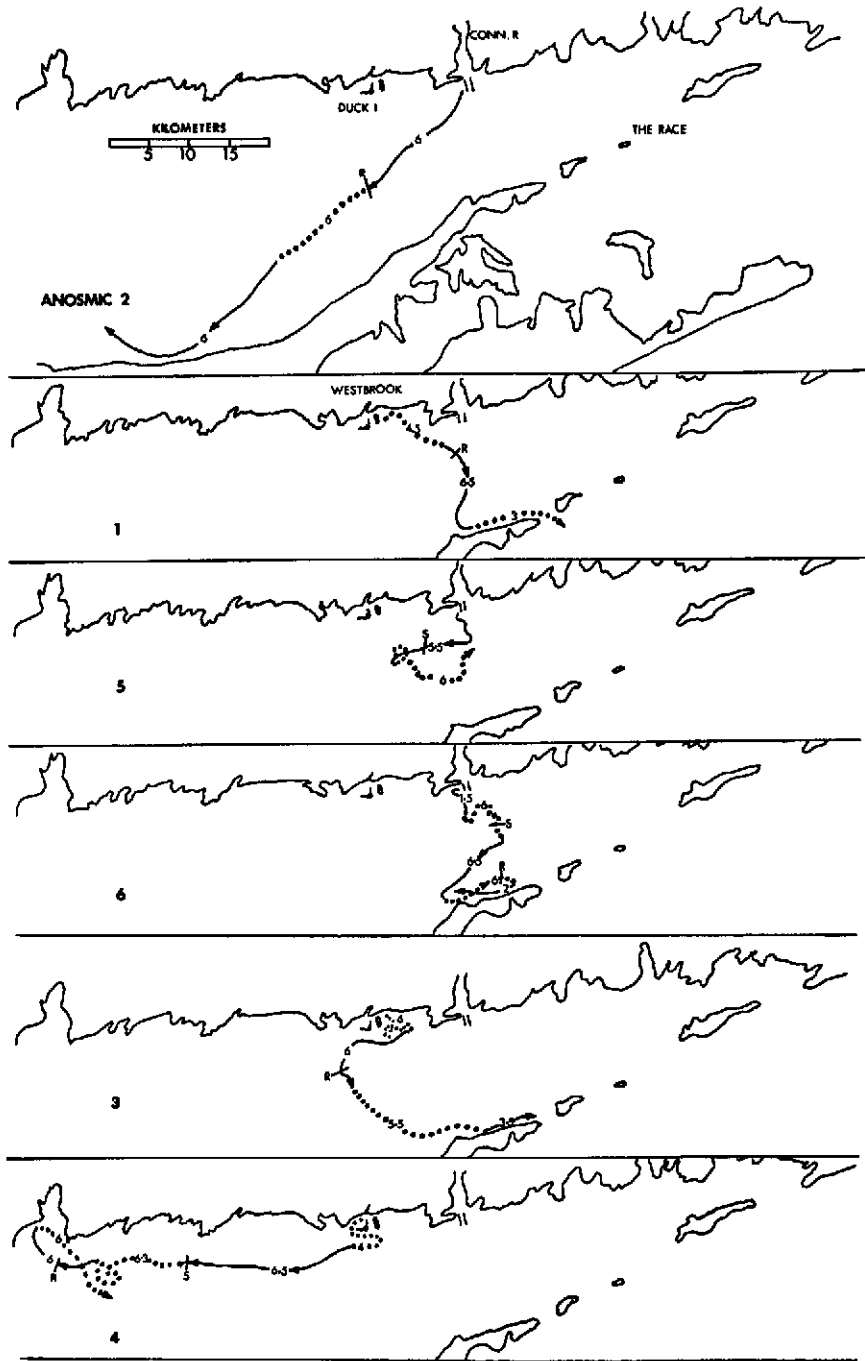


FIG. 2. Migration routes of six anosmic sonic-tagged American shad (*Alosa sapidissima*) tracked in Long Island Sound in 1972. Solid line represents fish displacement during flood tide, dotted line during ebb tide. Numbers represent time in hours during the indicated tidal condition. R — point of observed sunrise; S — point of observed sunset.

conditions. Blind shad 2, 3, and 5 all moved west during both tidal conditions, blind shad 4 moved east during both tidal conditions, and blind shad 1 moved east during ebb tide and west during flood tide.

Five of seven blind/anosmic shad were tracked continuously following release (Fig. 4). Of the remaining two, one was lost due to poor weather conditions and one was lost due to equipment

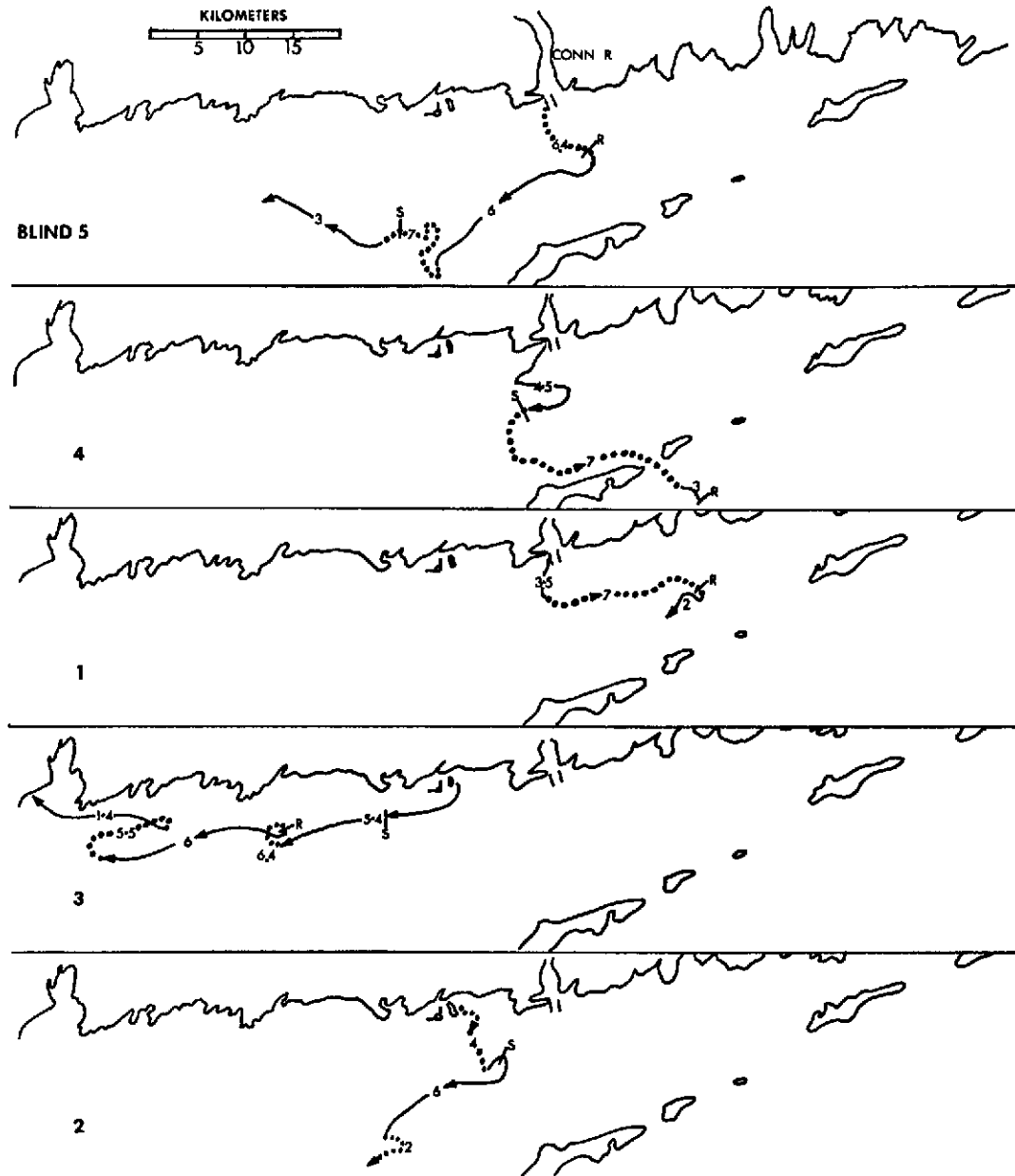


FIG. 3. Migration routes of five blind sonic-tagged shad tracked in Long Island Sound in 1972. Solid line represents fish displacement during flood tide, dotted line during ebb tide. Numbers indicate time in hours during the indicated tidal condition. R — point of observed sunrise; S — point of observed sunset.

failure. Blind/anosmic shad 1 moved west during both tides while the remaining four moved west during flood tide and east during ebb tide.

Behavior — Response to tidal current direction
— Current directions and headings of sensory impaired shad were calculated over 15- and 30-min

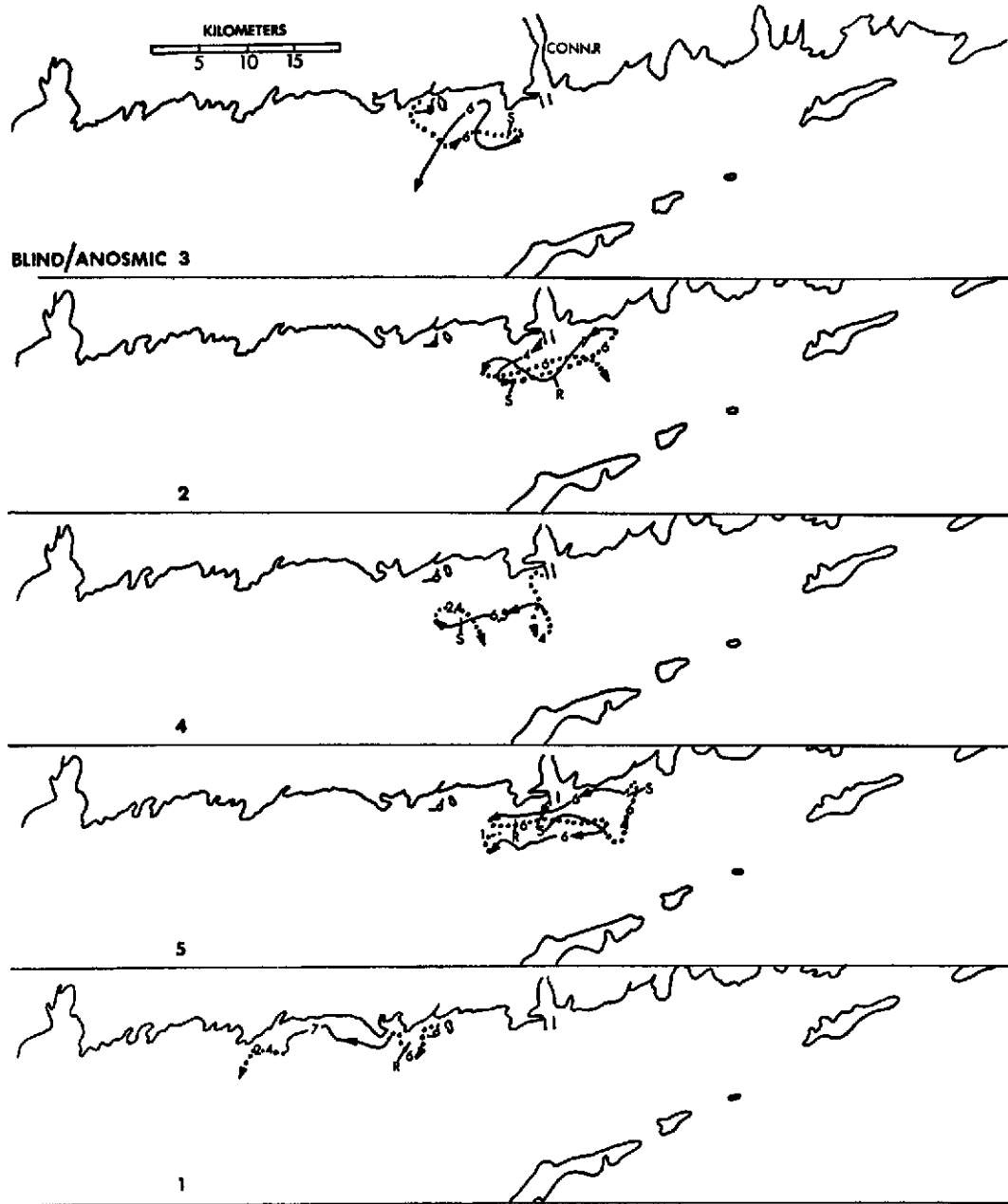


FIG. 4. Migration routes of five blind/anosmic sonic-tagged shad tracked in Long Island Sound in 1972. Solid line represents fish displacement during flood tide, dotted line during ebb tide. Numbers represent time in hours during the indicated tidal condition. R — point of observed sunrise; S — point of observed sunset.

time increments and the data for each category of sensory-impaired shad was pooled. Anosmic shad headings and current directions were negatively correlated ($r = -0.25$, $n = 213$, $P < 0.01$). This tendency to orient into the reversing tide was equally significant during daylight and darkness. Blind shad headings and current directions were not significantly correlated ($r = -0.08$, $n = 142$, $P > 0.1$). Blind/anosmic shad headings and current directions were negatively correlated ($r = -0.25$, $n = 194$, $P < 0.01$). The tendency of blind/anosmic shad to orient into the current was more significant during daylight ($r = -0.27$, $n = 122$, $P < 0.01$) than

darkness ($r = -0.16$, $n = 72$, $P > 0.1$). Mean fish headings during ebb and flood tide conditions were plotted against mean ebb and flood tide current directions and are shown for each category of sensory-impaired shad in Fig. 5.

Changes in the headings of impaired shad at successive positions along the tracks (turning angles) were calculated for each shad tracked in 1972 and analyzed within each category of sensory impairment for the frequency of large turning angles ($>45^\circ$) exhibited during ebb and flood tide conditions. The pooled data for each impairment category revealed no significant differences in the

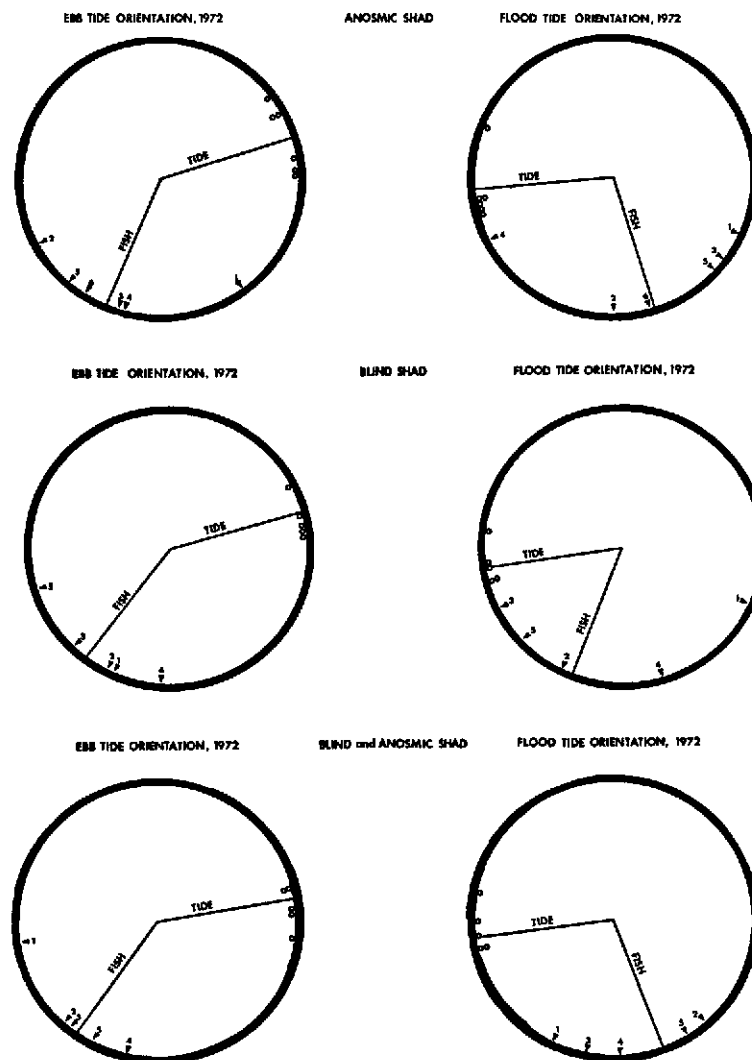


FIG. 5. Individual mean fish heading and tide direction for anosmic, blind, and blind/anosmic shad tracked in Long Island Sound in 1972.

TABLE 2. The frequency of large turning angles ($>45^\circ$) calculated during ebb and flood tide conditions and pooled for each category of sensory-impaired shad tracked in Long Island Sound in 1972.

Fish treatment	Ebb tide		Flood tide		χ^2	P
	n	turning angles $>45^\circ$	n	turning angles $>45^\circ$		
Anosmic	111	57	94	42	0.32	>0.1
Blind	70	42	66	38	0.02	>0.1
Blind/anosmic	86	54	102	63	0.01	>0.1

frequency of large turning angles between ebb and flood tide conditions (Table 2). The frequencies of large turning angles exhibited by each impaired shad tracked in 1972 are presented in Table 3.

Response to Tidal Current Rate

The calculated swimming speeds of impaired shad, similarly based on 15- and 30-min time increments, were pooled within each category of sensory impairment and analyzed in relation to the rate of the ebb and flood tide currents. Anosmic shad swimming speeds were positively correlated with tidal current rate ($r = 0.24$, $n = 224$, $P < 0.01$). This relationship was equally significant during daylight and darkness. Increases in current rate

during the ebb tide produced greater increases in swimming speed ($b = 0.367$) than did similar increases in current velocity during the flood tides ($b = 0.278$). No significant correlation was found between the calculated swimming speed of blind shad and tidal current rate ($r = -0.02$, $n = 148$, $P > 0.1$). Calculated swimming speeds of blind/anosmic shad were positively correlated with tidal current velocities ($r = 0.201$, $n = 206$, $P < 0.01$). This relationship was more significant during daylight ($r = 0.18$, $n = 128$, $P < 0.05$) than darkness ($r = 0.14$, $n = 78$, $P > 0.1$), but did not differ between ebb and flood tides.

Anosmic shad and blind shad swam at speeds greater than both tidal current rates. Blind/anosmic shad swam at speeds not significantly different from tidal current rates (Table 4).

The mean calculated swimming speeds of each sensory-impaired shad tracked during ebb and flood tide conditions in 1972 are presented in Table 5.

The observed swimming speeds of anosmic shad were positively correlated to surface salinities ($r = 0.24$, $n = 118$, $P < 0.05$) but were not correlated to temperature. Neither blind shad nor blind/anosmic shad exhibited any significant correlation between observed swimming speed and surface salinity or temperature.

Discussion

Unimpaired sonic-tagged shad tracked in Long Island Sound in 1970 and 1971 exhibited two major open water behavioral parameters; they tended to head into the reversing tidal current at all times and they altered their swimming speeds in relation to changes in tidal current velocities. This behavior, however, was not quantitatively equivalent during ebb and flood tide conditions. All unimpaired shad tracked in 1970 and 1971 headed into the ebb tide whereas during the flood tide, their orientation ranged from countercurrent to concurrent. This situation was reflected in the smaller frequency of

TABLE 3. The frequency of large turning angles ($>45^\circ$) exhibited by each sensory-impaired shad during ebb and flood tide conditions.

Fish treatment	Fish no.	Release date	% large turning angles	
			Flood tide	Ebb tide
Anosmic	01	Apr. 25	16.6	85.7
	02	May 5	69.2	25.0
	03	May 7	36.8	33.3
	04	May 21	47.1	70.4
	05	May 24	42.9	66.7
	06	June 1	52.6	41.7
Blind	01	Apr. 27	62.5	50.0
	02	Apr. 29	33.3	60.0
	03	May 12	77.3	63.6
	04	May 23	50.0	57.1
	05	May 30	41.7	60.0
Blind/anosmic	01	May 2	50.0	42.8
	02	May 10	50.0	68.2
	03	May 18	71.4	72.7
	04	May 26	75.0	38.5
	05	June 3	66.7	69.7

large turning angles exhibited by unimpaired shad during the ebb tide than during the flood tide. Increases in the rate of the ebbing tide resulted in greater increases in swimming speed than did similar increases in the rate of the flooding tide. This situation was reflected in the greater magnitude of swimming speeds while heading west during the ebb tide than during the flood tide. This combination of orientation and swimming behavior resulted in a net westerly displacement in Long Island Sound. Forty of 43 unimpaired shad tracked in 1970 and 1971 effected a net westerly movement during the ebb tide and either held their position

or were slowly carried west by the flood tide (Dodson and Leggett 1973).

Anosmic and blind/anosmic sonic-tagged shad exhibited the same two major parameters characteristic of the behavior of unimpaired shad. This behavior, however, was equivalent during both tides. The pooled data for anosmic shad and for blind/anosmic shad revealed no differences in the frequency of large turning angles during ebb and flood tides. Furthermore, anosmic shad swam at speeds in excess of both tidal rates and blind/anosmic shad swam at speeds approximately equal to both tidal current rates. Therefore, anosmic and blind/

TABLE 4. Mean tidal rates and mean calculated swimming speeds of sensory-impaired sonic-tagged shad (pooled for each category of sensory impairment).

Fish treatment	Flood tide						Ebb tide					
	n	tidal rate (cm/s)		swimming speed (cm/s)		t-test P	n	tidal rate (cm/s)		swimming speed (cm/s)		t-test P
		mean	SD	mean	SD			mean	SD	mean	SD	
Anosmic	98	53.6	26.5	76.5	33.5	<0.01	115	53.0	32.6	81.4	45.7	<0.01
Blind	70	50.3	28.9	74.1	54.9	<0.01	72	52.1	28.7	68.6	45.7	<0.02
Blind/anosmic	105	47.2	19.8	47.9	26.8	>0.05	89	53.9	26.8	61.6	36.6	>0.05

TABLE 5. Mean tidal rate and mean calculated swimming speed of individual sonic-tagged sensory-impaired shad tracked in Long Island Sound in 1972 during ebb and flood tide conditions.

Fish treatment	No.	Flood tide				Ebb tide			
		n	mean tidal rate (cm/s)	mean swim speed (cm/s)	P	n	mean tidal rate (cm/s)	mean swim speed (cm/s)	P
Anosmic	01	12	72.5	99.1	<0.05	8	82.9	75.6	>0.05
	02	16	59.1	85.7	<0.05	12	53.3	138.4	<0.01
	03	19	53.6	66.5	>0.05	19	58.8	74.4	>0.05
	04	17	34.1	73.8	<0.01	28	31.7	90.2	<0.01
	05	15	61.9	79.6	>0.05	12	74.7	90.2	>0.05
	06	19	47.2	64.9	>0.05	24	43.3	53.6	>0.05
Blind	01	7	55.8	48.8	>0.05	15	69.8	60.9	>0.05
	02	8	62.8	78.9	>0.05	5	56.1	66.5	>0.05
	03	24	55.5	73.8	>0.05	22	39.0	47.9	>0.05
	04	19	41.8	79.9	<0.01	15	65.2	78.9	>0.05
	05	12	42.4	73.2	<0.01	16	40.8	95.1	<0.01
B/A	01	12	43.6	42.4	>0.05	8	60.9	105.2	<0.02
	02	27	53.9	53.3	>0.05	22	64.3	42.4	<0.05
	03	7	43.9	72.9	<0.05	12	53.3	61.6	>0.05
	04	12	50.9	36.6	>0.05	14	53.6	85.3	<0.01
	05	47	43.6	45.1	>0.05	33	45.7	53.6	>0.05

anosmic shad failed to exhibit the westerly bias in behavior characteristic of unimpaired shad.

Analysis of the behavior of individual shad revealed that the apparent unbiased behavior of the anosmic group was the result of equal frequencies of westerly biased (anosmic shad 2 and 4), easterly biased (anosmic shad 1 and 3), and unbiased (anosmic shad 5 and 6) behavior. Four of five blind/anosmic shad exhibited no unidirectional bias in behavior. Only blind/anosmic shad 1 exhibited a westerly movement.

Blind shad failed to exhibit the tendency to head into the tidal current or the adjustment of swimming speeds relative to changes in tidal current velocity. The orientation of blind shad, however, was not equivalent during both tidal conditions. While tending to head into the ebb tide, blind shad exhibited concurrent and crosscurrent orientation during flood tide that resulted in a net westerly movement (blind shad 2, 3, and 5).

In an earlier paper (Dodson and Leggett, 1973) we proposed that two sets of environmental clues were used by shad in locating their home river. We distinguished between those clues used by shad to respond to changes in tidal current rate and direction and those responsible for establishing the westerly bias in behavior which resulted in movement from the Atlantic Ocean west toward the Connecticut River. The tracking of sensory-impaired shad in 1972 partially supports such a hypothesis. Deprivation of olfactory clues impaired shad's ability to maintain a consistent westerly bias and subsequent westerly displacement without eliminating the open water behavior patterns characteristic of the behavior of unimpaired shad. However, deprivation of visual clues impaired shad's ability to behave in a similar manner to unimpaired shad without eliminating their ability to maintain a westerly displacement in Long Island Sound.

The tracking of blind/anosmic sonic-tagged shad illustrated that the distinction between the roles of vision and olfaction in establishing the observed behavior is not clear. The fact that four of six anosmic shad exhibited some form of unidirectional bias in orientation whereas only one of five blind/anosmic shad did so suggests that visual clues may be involved in maintaining a directional bias. In addition, the observed ability of blind/anosmic shad to exhibit the 2 major parameters of behavior characteristic of unimpaired shad suggests that visual clues are not solely responsible for detection of changes in current rates and direction.

The tendency of anosmic shad to orient at right angles to the ebbing tide resulted in four of six anosmic shad migrating to the south shore of Long Island Sound. Only one unimpaired shad

followed a similar path. In addition, few shad are caught along the south shore of Long Island Sound as no major tributaries are located there (Walburg and Nichols 1967). This southerly movement may have resulted from a search for olfactory clues indicative of the Connecticut River. The observed swimming speeds of anosmic shad decreased when surface salinities declined whereas unimpaired sonic-tagged shad increased their observed swimming speeds under similar conditions (Dodson and Leggett 1973). This behavior may have resulted from attempts by anosmic shad to search out olfactory clues normally associated with reduced salinities.

The net westerly movement of unimpaired shad tracked in 1970 and 1971 caused these fish to move west beyond the Connecticut River. The fact that both sonic-tagged and dart-tagged shad were subsequently recaptured in the Connecticut River indicates that this westerly bias was reversed at some point along the migration. Three unimpaired shad tracked in 1970 exhibited such a reversal resulting in easterly movement toward the Connecticut River. We proposed (Dodson and Leggett 1973) that the environmental clues responsible for establishing the initial westerly bias were also responsible for reversing the bias leading to movement toward the river once it had been passed. The reduced ability of blind/anosmic shad and anosmic shad to locate the home river, and the observed ability of blind shad to home from 10 km away without a significant reduction in success suggests that olfactory clues are instrumental in initiating the initial westerly bias and, subsequently, reversing this bias. The reduced homing ability of blind shad released at Saybrook is difficult to account for. Visual clues do not appear to become more important as the river is approached because blind shad homed successfully from Westbrook. Further work is required to identify the reasons for this result.

The observed differences between the behavior of sensory-intact shad tracked in 1970 and 1971 (Dodson and Leggett 1973) and sensory-impaired shad tracked in 1972 could have resulted from annual differences in environmental conditions and/or the motivational state of shad.

If the overall behavior of the annual population was affected by such factors we would expect the changes to be reflected in the timing of the shad run in the Connecticut River, and possibly also in the average rate of upriver migration.

Catch/effort data from an experimental gillnet fished daily at the mouth of the Connecticut River throughout the shad runs of 1970 to 1972 revealed that the date of the first shad capture varied by only 1 day and the date of the median shad capture

by only 4 days over the 3 yr. In addition the rate of upriver migration was similar, with the largest difference occurring between 1970 and 1971 when unimpaired fish were being tracked (1970 — 2.7 km/day; 1971 — 2.3 km/day; 1972 — 2.4 km/day; W. C. Leggett unpublished data). River discharge volumes during April and May varied during the period, but the differences were small (1970 — 47.6×10^3 cfs average; 1971 — 46.1×10^3 cfs average; 1972 — 53.1×10^3 cfs average). The greatest difference between the years occurred in population size (1970 — 730,000; 1971 — 705,000; 1972 — 397,000); however, these population fluctuations are known to have resulted from differences in recruitment and escapement (W. C. Leggett unpublished data) and do not appear to be influenced by environmental factors (Fredin 1954; W. C. Leggett unpublished data). In addition the frequency of recovery and mean homing times of unimpaired shad released in Long Island Sound in 1971 and 1972 did not differ significantly. While the possibility remains that behavioral changes could have occurred without altering the above population characteristics we feel a more tenable conclusion is that the observed differences in behavior of unimpaired and impaired shad resulted from sensory impairment.

It is also possible that sensory impairment may have caused differences in behavior that transcend the loss of the cue or sense. Peters (1971) noted the possibility that olfactory impairment may affect behavior patterns not directly associated with odor stimuli. However, removal of the olfactory bulbs has not resulted in deficits in reproductive behavior, parental activities, aggressive behavior, or schooling (Aronson 1970). In this study, sensory mutilation was avoided and shad were not held or displaced after the sensory occlusions, but were released immediately in an attempt to minimize possible traumatic effects and behavior modifications related to handling and occlusion.

The available data indicate that an olfactory-rheotactic mechanism forms the basis of the non-random search pattern displayed by unimpaired Connecticut River shad in locating their home river. The westerly bias in the open water migration characteristic of unimpaired shad entering Long Island Sound appears to be most directly governed by olfactory clues emanating from the Connecticut River while the unidirectional displacement is governed by reference to the rate and direction of the tidal currents. Behavioral and electrophysiological studies have demonstrated the ability of fish to detect low concentrations of odor, and to discriminate one or more odors in a mixture. They have also implicated olfactory clues in the process of parent stream recognition (Kleerekoper 1969;

Harden-Jones 1968; Hara 1970). However, to guide fish directly to their home river the concentration gradient of the odor must be sufficiently steep to elicit a kline or tropotaxis (Hara 1970). Such steep gradients do not exist in Long Island Sound where the strong reversing currents dilute and disperse home river clues both to the east and west of the Connecticut River. The historical and present abundance of shad west of the Connecticut River during spawning migrations (Walburg and Nichols 1967) and the observed westerly movement of shad already west of the Connecticut River supports this view.

The response by shad to changing water velocities and current directions is less clearly defined. Water currents may provide unambiguous directional clues to migrating fish but the sensory pathways involved in orientation is a point of considerable speculation. In this study visual clues were implicated but were clearly not solely responsible for the rheotaxis. Semicircular canals (Gray 1937), electromagnetic clues (Royce et al. 1969), and tactile clues (Harden-Jones 1969) have been suggested as possible alternatives to sight. No evidence exists to evaluate the ability of shad to utilize such cues.

The results of the present study lead us to the following hypothesis concerning the homing migration of American shad. The cyclical and precisely timed nature of their extensive oceanic migration (Leggett and Whitney 1972) brings both mature and immature shad into the vicinity of their home river and of the characteristic odors of the system once a year.

In the case of Connecticut River shad, Connecticut River water has been detected off Montauk Point (Riley, 1959) well within the proposed oceanic migration route of the species. At this point olfactory clues, indicative of the Connecticut River act as a positive reward in a conditioning process whereby shad moving to the west are rewarded by remaining within the detectable odor field, those moving to the east are not.

Immature shad are believed to migrate with the adults at sea (Talbot and Sykes 1958). Since immature shad do not join in the spawning migration, it is possible that the onset of sexual maturity is directly related to the perception and/or recognition of the olfactory stimulus. The hormonal state of the animal in relation to gonad development could operate to moderate this response.

Once the required westerly bias is established, reference to the tidal currents provides the necessary directional information and maintains the fish on an east-west axis. Once established, the westerly bias in behavior would continue until the river is reached or, as apparently happens in a great many instances, the shad move west beyond the river and

the limits of its odor plume. In the latter instance another reward-non-reward conditioning process may establish an easterly bias leading to movement in the direction of the river. This sequence of westerly and easterly movements may occur several times before the river is located. This would explain the relatively long homing times from distances as short as 10 km. Eventual recognition of the home river appears to involve both olfactory and visual clues.

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