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PRIMARY RESEARCH PAPER

What is "fallback"?: metrics needed to assess telemetry tag effects on anadromous fish behavior

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Abstract Telemetry has allowed researchers to document the upstream migrations of anadromous fish in freshwater. In many anadromous alosine telemetry studies, researchers use downstream movements ("fallback") as a behavioral field bioassay for adverse tag effects. However, these downstream movements have not been uniformly reported or interpreted. We quantified movement trajectories of radio-tagged anadromous alewives (*Alosa pseudoharengus*) in the Ipswich River, Massachusetts (USA) and tested blood chemistry of tagged and untagged fish held 24 h. A diverse repertoire of movements was observed, which could be quantified using (a) direction of initial movements, (b) timing, and (c) characteristics of bouts of coupled upstream and downstream movements (e.g., direction, distance, duration, and speed). Because downstream movements of individual fish were almost always made in combination with upstream movements, these should be examined together. Several of the movement patterns described here could fall under the traditional definition of "fallback" but were not necessarily aberrant. Because superficially similar movements could have quite different interpretations, post-tagging trajectories need more precise definitions. The set of metrics we propose here will help quantify tag effects in the field, and provide the basis for a conceptual framework that helps define the complicated behaviors seen in telemetry studies on alewives and other fish in the field.

Keywords Alosine · Tag effect · Movement · Behavior

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Introduction

Telemetry research using radio, acoustic, and passive integrated transponder (PIT) tags is important for anadromous fish research and management (McDowall, 1999; Lucas & Baras, 2000; Lassalle et al., 2008).

Tagging studies, however, are only useful if the tag does not alter fish behavior compared to untagged fish (Bridger & Booth, 2003; Rogers & White, 2007; Cooke et al., 2008). Identifying tag effects in the field is difficult because untagged fish cannot be tracked, and consequently the complex movements of untagged and tagged fish are difficult to compare. Although examining physiology and behavior of tagged and untagged fish in the laboratory is possible, such studies are time consuming, and confining migratory fish can cause additional stress.

In the northeastern United States, the closely related alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), collectively referred to as river herring, have historically and ecologically been an important component of coastal rivers. Tracking within-river movements of spawning adults of the genus *Alosa* is of special interest to many researchers and management agencies. Because anadromous shad and herring are sensitive to handling, researchers often use "fallback" (i.e., downstream movement of an upstream migrating anadromous fish following tagging) as a behavioral bioassay to document adverse tag effects on alosines (Beasley & Hightower, 2000; Hightower & Sparks, 2003; Bailey et al., 2004; Olney et al., 2006). Here, we use a literature review to show that the present language describing downstream movements is not standardized. Then, we illustrate the diversity of possible downstream movements. Finally, we propose a standardized series of metrics for quantifying post-tagging movements.

In the literature, many features of existing tagging studies on anadromous shad and herring are similar (Dodson et al., 1972; Bell & Kynard, 1985; Barry & Kynard, 1986; Chappelear & Cooke, 1994; Beasley & Hightower, 2000; Moser et al., 2000; Hightower & Sparks, 2003; Acolas et al., 2004; Bailey et al., 2004; Sprankle, 2005; Olney et al., 2006; Table 1). Of these, 81.8% focused on American shad (*Alosa sapidissima*), 9.1% examined blueback herring (*A. aestivalis*), and 9.1% used Allis shad (*A. alosa*). These studies either quantified fish passage (54.5%) or sought to understand migratory behavior (45.5%). All these studies used upstream migrating adult fish captured during the spawning run. All such studies were undertaken in river systems and most used fish obtained from fish passage structures (45.5%) or in-river capture (45.5%; no information provided 9.1%). Radio ("R", 54.5%) or acoustic ("A", 45.5%) tags were gastrically implanted (100%). With one exception, these studies were conducted without anesthetic (Acolas et al., 2004). Fish were typically released at the capture site (66.7%) or downstream of it (25.0%; no information provided, 8.3%).

Although the conditions of the studies were similar, individual researchers reported very different information about downstream movements post-tagging. The number of fish tagged (*N*) ranged from 7 to 110 (Table 1). All these studies reported some proportion of the study population to "fallback" (range, $n =$ 1–87 individual fish; 8.6–100% of the tagged fish in each study). While all these studies describe downstream movement, uniform terms were not used to quantify this behavior. The term "fallback" was used in 18.2% of the studies. This type of movement was also described by phrases such as "swam or passively drifted," "moved," "migrated," and "drifted" downstream, as well as "dropback" and "left the study area." In studies where quantitiative measures were reported, fish were listed as "falling back" when they moved downstream at times ranging from <1 to 168 h (7 days) post-release. In addition to the temporal frame of reference, the spatial focus of "fallback" activity was highly variable. The distance that fish moved downstream post-tagging in "fallback" activities ranged from <1 to 30 km. Of these studies, 45.5%, did not report a specific distance. While the majority of researchers (63.6%) included "fallback" fish in the data analyses as long as the fish returned upstream, 27.3% excluded "fallback" fish from analysis (no data reported, 9.2%). Hence, although the concept of downstream movement was embraced by most studies as a field diagnostic of adverse tag effects, how researchers quantified this behavior relative to time frame, spatial scale, and data analysis was variable, preventing comparisons across studies.

The interpretation of downstream movements of upstream migrating fish after tagging is an important issue and has significant consequences for field research, data analysis, and management. Unfortunately, our examination of the literature has shown that there is little consistency in how "fallback" is reported. Here, we use movement trajectories from our own field research on alosines to construct a conceptual framework for organizing the diversity of possible downstream movements. Specifically, we ask: (1) What types of downstream movements occur in upstream migrating anadromous alewives post-tagging? (2) Were tagged

Table 1 A review of alosine telemetry studies showing authors of study, species, purpose of the study, tag type, location of release site in relation to capture site, *N* released, *n* fallback, language used in the text to describe fallback, time period during which fish moved downstream (h), distance fish moved downstream (km), and whether "fallback" fish were excluded from analysis

Citation	Species	Purpose	Tag	Release in relation to capture	*N*	"Fallback"				
						n	Language	Time period (h)	Distance (km)	Excluded from analysis
Acolas et al. (2004)	Allis Shad	Behavior	A	Same or down	23	2	"Moved downstream"	≤24	≤1	Yes (mortality)
Bailey et al. (2004)	Am. Shad	Passage-up	R	NR	110	87	"Downstream movement"	≤168	1.3 to >30	No
Barry & Kynard (1986)	Am. Shad	Passage-up	R	Down	34	34	"Drop back"	<1	1–8	No
Beasley & Hightower (2000)	Am. Shad	Passage-up	A	Same	25	"Several"	"Fallback"	≤10	NR	No
Bell & Kynard (1985)	Am. Shad	Passage-down	R	Down	36	28	"Swam or passively drifted downstream"	≤8	0.7–16.5	No
Chappelear & Cooke (1994)	Blueback	Passage-up	R	Same	45	8	"Left the study area and never returned"	≤24	NR	Yes
Dodson et al. (1972)	Am. Shad	Behavior	A	Same	7	1	"Migrated downstream"	≤10	NR	–
Hightower & Sparks (2003)	Am. Shad	Behavior	R	Same	17	"Most"	"Movement downstream"	NR	NR	No
Moser et al. (2000)	Am. Shad	Passage-up	A	Same	86	"Most"	"Drifted downstream"	≤24	NR	No
Olney et al. (2006)	Am. Shad	Behavior	A	Same	29	13	"Unexpected movement downstream"	NR	≥7.4	No
Sprankle (2005)	Am. Shad	Behavior	R	Same	72	7	"Fallback"	72	≤1	Yes

Am. shad is American shad, blueback is blueback herring. Passage studies examined either upstream or downstream passage. Tags are represented by a single letter: acoustic or ultrasonic (A) or radio (R). NR indicates no explicit reporting of value. Dashes indicate a measure that is not applicable to that study

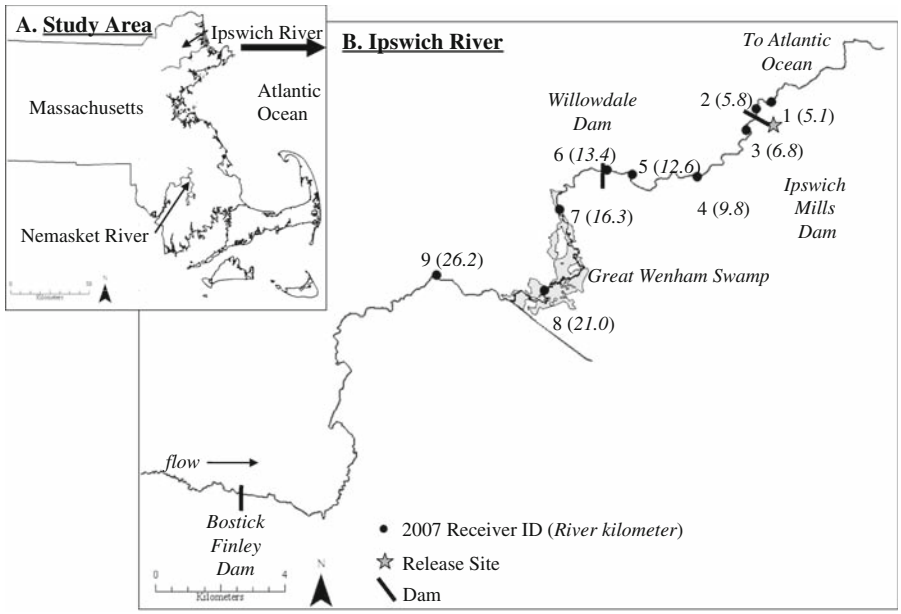

Fig. 1 **A** Map of the Nemasket and Ipswich Rivers in Massachusetts, USA. **B** Adult alewives volitionally migrating upstream in the Ipswich River were obtained, tagged, and released near the Ipswich Mills Dam [river kilometer (rkm) 5.9] and tracked through nine stationary receivers (rkm 5.1–26.2). *Black dots* indicate receivers. Text indicates receiver number and rkm in parentheses. The star indicates where fish were tagged and released at the Ipswich Mills Dam (rkm 5.8). The largest available spawning area is thought to be Great Wenham Swamp between receivers 7–8

fish more stressed than untagged fish? (3) What standardized metrics should be reported in future studies to allow comparisons across systems and fish? (4) Do downstream movements necessarily have adverse consequences?

Materials and methods

The Ipswich River is a 72.4-km, fifth-order river in northeastern Massachusetts that empties into the Atlantic Ocean through Plum Island Sound (Fig. 1). Three low-head dams (1.4–2.0 m spillway height) with varying degrees of passage are present in the mainstem. Ipswich Mills Dam [river kilometer (rkm) 5.9] has a Denil fish ladder and Willowdale Dam (rkm 13.7) has a notched weir–pool fishway. Bostik-Finley Dam (rkm 41.2) has no passage and represents the upper limit of anadromous fish range in the river. Historically, river herring spawned in the 0.9 km^2 Wenham Lake, now a municipal water supply that is inaccessible to fish. At present, the largest available alewife spawning habitat is Great Wenham Swamp, an extensive wetlands upstream of Willowdale Dam covering 6.47 km^2. Temperatures during the period of alewife migration, averaged 13.5°C (SE = 1.3, range 6.1–16.1) and mean discharge was 21.9 $m^3\ s^{-1}$ (SE = 3.4, range 13.1–38.9).

For tagging, adult alewives were captured in the Ipswich Mills Dam fishway (rkm 5.9) using a box trap placed at the upstream fishway exit. The trap (61 cm high, 61 cm wide, 122 cm long) was checked at least once per day during the spring when it was fishing (55 fishing days in 2007, April 2–June 15). Only fish that appeared healthy and uninjured were tagged, and only those that recovered quickly from the tagging process were released.

Alewives ($n = 21$, mean TL = 267 mm, SE = 3.6) were tagged during April 23–27, 2007. After fish were obtained from the box trap, they were placed into a rectangular tank (31 cm wide, 64 cm long, 20 cm water depth) where they were gently caught by hand for tagging. We used radio tags (Model NTC-6-1 transmitters, Lotek Wireless, Newmarket, ON) that were 22.4 mm long, 9.1 mm diameter, weighing 2.8 g in air, with a calculated operational life of 124 days. On average, alewives weighed 175.0 g; hence, tags were less than the recommended maximum of 2% of

the body weight (Winter, 1996). Tags were individually coded and assigned to one of five frequencies. Within 30 s, tags were implanted gastrically, without the use of anesthetics. Using a hollow plastic insertion tool (12.3 cm long and 8 mm diameter tapering from 8 to 5 mm) the tag was inserted following the procedure described by Smith et al. (2009). Fish were then released at the capture location (rkm 5.9).

Nine stationary radio telemetry receivers (Model SRX_400, Lotek Wireless, Newmarket, ON) were located in the Ipswich River at rkm 5.1, 5.8, 6.8, 9.8, 12.6, 13.4, 16.3, 21.0, and 26.2 (Fig. 1B). Receiver gain was changed as needed during the study season. Receivers scanned all the frequencies in 5.5 s. Ranges for each receiver were determined prior to and after the release of tagged fish. The linear range extended up and downstream from 42 to 298 m. Receiver efficiency, the relationship between the detections of a tagged fish at a specific receiver divided by number of times that fish was detected by adjacent receivers above and below the target, was 88.7–100.0%. Receivers were downloaded two to four times per week. Data on fish movements were recorded from April 23 to June 5, 2007 (43 days).

We also examined plasma cortisol, glucose, and chloride ions of tagged and untagged alewives from the Nemasket River (Fig. 1) using the same protocol. For this physiological assay, fish were dipnetted from the Wareham Street Dam fishway (rkm 12.1) on April 30, 2007 ($n = 20$). One to two fish were captured from the fishway at a time. After netting, fish were placed in a cylindrical holding tank (113 l; 0.6-m diameter, 0.6-m height) filled with ambient river water. From this tank, individual fish were collected one at a time with a smaller net. Blood was drawn from each fish's caudal blood vessels using a heparinized syringe. After blood collection, fish were euthanized. The entire blood collection process was completed within 5 min of the time each individual fish was captured in the fishway. Blood samples were kept on ice until all the fish were sampled, then samples were centrifuged at 2,000*g* for 5 min. Plasma was decanted and frozen on dry ice and stored at −80°C until it could be analyzed in the laboratory.

In order to measure stress in response to tagging, we inserted dummy tags (22.4 mm long and 9.1 mm in diameter, weight in air = 2.8 g) into 10 alewives using the methods described above. An additional 10 alewives were removed from the river and handled but not tagged. Two pairs of tagged and untagged fish were placed in each of five cylindrical mesh net pens (61 cm in diameter, 61 cm deep, 64 cm mesh) anchored in a still section of the Nemasket River at a depth of 1.5 m. After fish had been in the pens for 24 h, we assessed survival and took blood samples. At 24 h, all fish were removed from a single pen using a dipnet and placed in a cylindrical holding tank (113 l; 0.6-m diameter and 0.6-m height) filled with ambient river water. Blood was drawn from each fish as described above within 5 min of the initial disturbance of each pen. Each pen was processed sequentially.

Plasma cortisol, glucose and chloride ions were analyzed at the USGS Conte Anadromous Fish Research Center (Turners Falls, MA, USA). Plasma cortisol was measured by direct enzyme immunoassay (Carey & McCormick, 1998) which has been validated for use in alosines (Shrimpton et al., 2001). Glucose was measured by the hexokinase and glucose-6-phosphate dehydrogenase enzymatic method using external standards (Stein, 1963). Plasma chloride was analyzed by the silver titration method using a Buchler-Cotlove digital chloridometer and external standards. One tagged fish did not yield enough blood to analyze the sample for chloride ions. We used multiple, nonparametric Mann-Whitney procedures (PROC NPAR1WAY, SAS 9.1) to test for differences in plasma cortisol, glucose and chlorides (1) between tagged and untagged alewives held 24 h, and (2) between all the unheld fish sampled initially and all the handled fish (tagged and untagged).

Results

Movements

We describe below movement trajectories of tagged alewives to illustrate the diversity of possible movement patterns. In general, we cite each trajectory for a single type of movement but most natural trajectories are complex combinations of multiple movements. We show all the 21 fish tagged in 2007. Our goal, however, was not to provide a quantitative analysis of fish movements, but to use individual fish trajectories to demonstrate the array of movements that may be encountered in the field.

Anadromous alewives differed in timing and direction of the initial movements (Fig. 2A–H), the

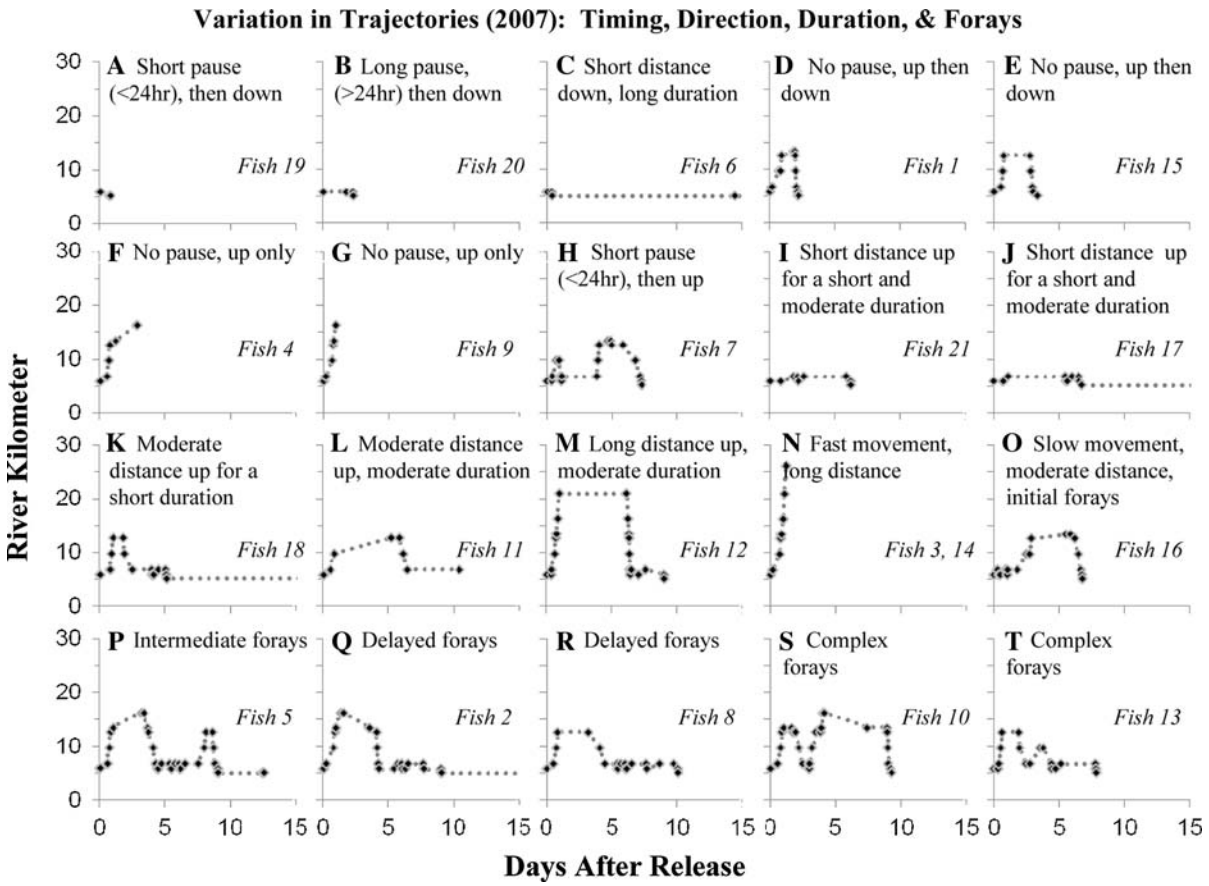

Fig. 2 Individual locations (river kilometer) and detection times (days after release) recorded for anadromous alewives caught and tagged during their spring upriver spawning migration in the Ipswich River, 2007. Individual fish are shown below to indicate real movement trajectories. **A** Short pause then downstream movement (Fish 19); **B** Pause lasting >24 h followed by downstream movement (Fish 20); **C** Short distance (<1 km) down, long duration (>24 h) (Fish 6); **D**, **E** No pause, up then down (Fish 1, 15); **F**, **G** No pause, up only (fish does not return downstream) (Fish 4, 9); **H** Short pause (<24 h), then up (Fish 7); **I**, **J** Short distance up for a short and moderate duration (Fish 21, 17); **K** Moderate distance up for a short duration (Fish 18); **L** Moderate distance up, moderate duration (Fish 11); **M** Long distance up, moderate duration (Fish 12); **N** Fast movement over a long distance (Fish 3, 14); **O** Slow movement, moderate distance, with initial forays (Fish 16). **P** Intermediate forays (Fish 5); **Q**, **R** Delayed forays, following a long distance migration (Fish 2, 8); **S**, **T** Complex forays (Fish 10, 13). *Dotted lines* indicate that locations between receivers are unknown. All upstream migrating fish tagged in 2007 are shown

duration, distance, and speed of initial movements (Fig. 2I–O), and patterns of forays or movement reversals (Fig. 2P–T). Most of the movement trajectories of individual fish included both upstream and downstream movements. The timing and direction of the first movement following release varied, with fish moving from the tagging site both downstream (Fig. 2A–C) and upstream (Fig. 2D–H). We observed downstream movement after a short pause (16.8 h after release, Fig. 2A) and also after a longer pause (55.2 h after release, Fig. 2B). Some fish that initially moved downstream stayed within our array briefly and then exited the receiver array for the duration of the study (Fig. 2A–B). Others that moved downstream stayed within the lower part of the array for a prolonged time (Fig. 2C). We also observed upstream directed movements immediately post-release (Fig. 2D–G), as well as following a short pause (<11.0 h, Fig. 2H–J). In most cases (Fig. 2D, E, H), but not all (Fig. 2F–G), initial upstream movements were followed by a return downstream.

We also examined the distance (km traveled in a single direction, i.e., Y-axis trajectory), duration (how long the fish was heard by a single receiver, i.e.,

X-axis trajectory), and speed (i.e., slope) of subsequent movements. Because we had data only for time at a receiver, we hypothesized interim movements by connecting these detections with a dotted line. We defined a movement event as the trajectory resulting from coupled bouts of adjacent upstream and downstream movements. Fish initially traveling upstream post-release moved short (Fig. 2I–J), moderate (Fig. 2K–L), and long distances upstream (Fig. 2M–N). For fish traveling a short distance upstream (<1 km from release site receiver; Fig. 2I–J), the duration of time spent upstream was both short (0.1 h) and moderately long (9.0 h, Fig. 2I–J). Similarly, fish traveling a moderate distance upstream (Fig. 2K–L), stayed short (Fig. 2K) and moderately long (Fig. 2L) durations at the upstream site. Other fish travelled long distances upstream (15.1 km from release site) and remained for a moderate period of time before returning downstream (Fig. 2M). Fish traveled upstream both at faster (1.02 km/h, Fig. 2N), and slower speeds (Fig. 2O).

Fish often reversed the direction of their movements (Fig. 2O–T). These forays occurred at different periods of the migration. Repetitive short distance upstream and downstream forays preceded longer-distance migrations upstream (Fig. 2O), occurred in the middle (Fig. 2P), or occurred at the end of the migration (Fig. 2Q–R). Other fish made multiple long-distance directional bouts of movement during their migration combining many directions and distances (Fig. 2S–T).

The above descriptions characterize select components of individual movement trajectories. Each complete trajectory was composed of three parts: (a) timing and direction of first initial movements; (b) distance, duration, and speed of subsequent bouts of coupled upstream and downstream movements, and (c) multidirectional forays (Table 2). Some similarities and some differences occurred when these components were summarized across trajectories. Out of 21 trajectories recorded in 2007, three had only a downstream component (Fig. 2A–C), three had only an upstream component (Fig. 2F, G, N), but the majority ($n = 15$; 71.4%) had both an upstream and downstream component associated with each bout of coupled upstream–downstream movements. Of these, three (Fig. 2D, E, L) had a single upstream–downstream trajectory whereas all the others had multiple bouts of upstream and downstream

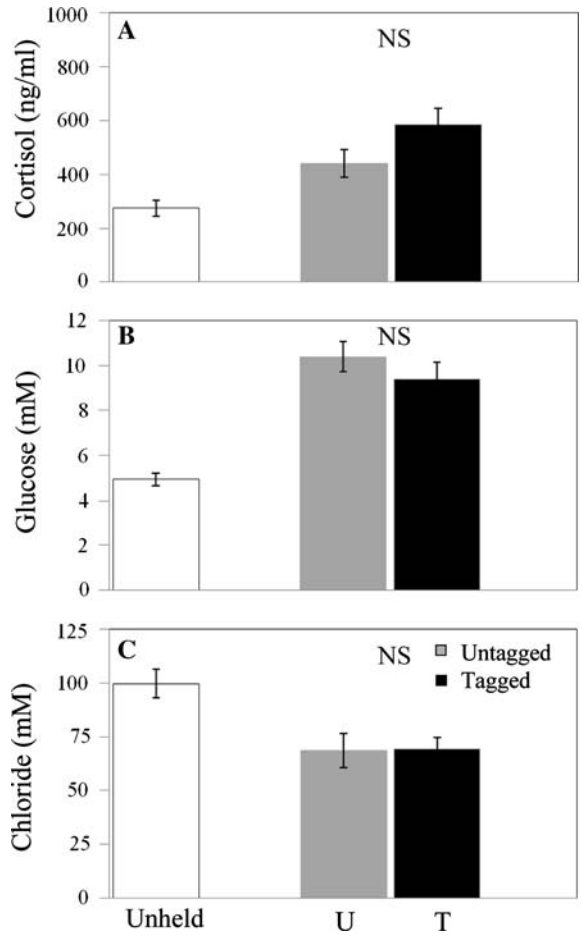

Fig. 3 Plasma **A** cortisol (ng/ml), **B** glucose (mM), and **C** chloride (mM) ion responses of unheld, untagged (U), and tagged (T) fish. Unheld, pre-tag levels were obtained before any activity occurred. The tagged and untagged fish were sampled at 24 h. NS indicates no significant difference between tagged and untagged fish. Data are mean ± 1 SE. Statistics are shown in Table 3

movements (Fig. 2H–K, M, O–T). In some of these multiple-maxima trajectories, distance traveled in both bouts of upstream and downstream movements were approximately equal in distance but differed in duration (Fig. 2P, S). In others, the distance and duration in one bout of movements were greater than the other (Fig. 2H, K, T). Still others included multiple, small, short forays (Fig. 2I–K, O–R). While we cannot neatly group fish that exhibited identical behaviors to characterize "normal" in the entire tagged group, use of these metrics would enable us start to systematically describe complicated fish movements (Table 2).

Table 2 Trajectories of each anadromous alewife tagged in 2007 broken down by three components: (a) timing and direction of initial movement indicating whether there was no, a short, or a longer pause in both downstream (down) and upstream (up) directions; (b) distance, duration, and speed of subsequent post-release movements in both the up and downstream directions including distance moved (short, moderate, or long), duration of time spent at extreme locations (short, moderate, long), and speed of movement (fast or slow); (c) forays or repeated short duration movements (initial or delayed). Components a and b are analyzed for all major peaks. The related figure panel is also indicated

Fish	a. Timing and direction of first post-release movement						b. Distance, duration, and speed of subsequent postrelease movements														c. Forays		Figure
	Down			Up			Up						Duration			Down					Initial	Delayed	
	Pause			Pause			Distance			Speed			Short	Moderate	Longer	Distance			Speed				
	None	Short	Longer	None	Short	Longer	Short	Moderate	Long	Fast	Slow					Short	Moderate	Long	Fast	Slow			
19		X											X			X							2A
20			X										X			X							2B
6		X													X	X							2C
1				X				X			X		X				X			X			2D
15				X				X			X			X			X			X			2E
4				X				X			X		X										2F
9				X				X			X		X										2G
7					X			X			X		X	X			X			X	X		2H
21					X		X				X		X	X		X				X			2I
17					X		X				X		X	X		X				X		X	2J
18				X				X			X		X				X			X		X	2K
11				X				X			X	X		X			X			X			2L
12					X					X	X			X			X			X		X	2M
3				X						X	X		X										2N
14				X						X	X		X										2N
16				X				X				X		X			X			X	X		2O
5				X				X			X	X	X	X			X			X		X	2P
2				X				X			X			X			X			X		X	2Q
8				X				X			X			X			X			X		X	2R
10				X				X			X		X	X			X			X			2S
13				X			X	X			X		X	X		X	X			X			2T

Table 3 Mann–Whitney test results for the effect of tagging on plasma cortisol, glucose, and chloride ion concentrations ($N = 20$)

Chemical	n	df	F value	P
Cortisol	20	18	3.25	0.09
Glucose	20	18	0.94	0.35
Chloride	19	17	0.01	0.92

Results indicate no difference in plasma concentrations between tagged and untagged fish held 24 h in the Nemasket River

Physiology

All tagged and untagged fish held in net pens were alive at 24 h. Plasma cortisol (Fig. 3A), glucose (Fig. 3B), and chloride ions (Fig. 3C; Table 3) did not differ between tagged and untagged fish. However, handling and confinement, whether associated with tagging or not, altered plasma cortisol, glucose, and chloride for both untagged and tagged fish compared to unheld, pre-tagging values (Fig. 3; $P < 0.001$ for cortisol, glucose, and chloride ions).

Discussion

We observed a diverse repertoire of downstream movements. Some fish moved downstream immediately; others moved downstream after a considerable period of upstream activity. Some fish moved at fast speeds; others moved more slowly. Some fish moved downstream and stayed there for a considerable period of time; others moved both downstream and upstream after both short and long pauses. Movements typically occurred in combination with upstream movements, so bouts of adjacent upstream and downstream movements should be examined together. Several of the movement patterns described here could fall under the traditional definition of "fallback" but were not necessarily an adverse reaction to tagging, and may, in fact, not have undesirable consequences. These patterns may represent the normal diversity of movements in pre-spawning river herring.

All trajectories can be quantified by (a) direction and time of initial movements, (b) distance traveled, speed, and time spent at a specific location for each coupled bout of adjacent upstream and downstream movements, and (c) number, type, and sequence of movement events. Because numerous possible explanations exist for this wide range of movements, the following issues should be addressed in future telemetry studies. First, researchers should note the context of the fish prior to capture. For all of the alosine telemetry studies under review in our study, anadromous fish were actively moving upstream prior to capture and tagging. When this is not the case, different interpretations of upstream and downstream movements may exist. Second, the location of the release site should be specified relative to the capture site. Researchers should provide a distance from the river mouth for both capture and release sites and should consider the role of upstream or downstream displacement (Makinen et al., 2000). Past telemetry studies on anadromous alosines have focused on fish passage, so that fish capture and release sites were typically the same. As the behavior of spawning anadromous fish is evaluated for river restoration, this may not always be true. For example, to evaluate stocking as a way to supplement depleted populations, tagged fish may be released directly into upstream spawning areas, a strategy that could have radical implications for the interpretation of telemetry data. Third, we suggest that researchers report where spawning habitat is located relative to the release site. If fish are released directly into an appropriate spawning habitat, fish may not need to move until they are ready to emigrate following spawning. In this case, interpretations of movements would be quite different than if a fish is required to swim a distance upstream to access spawning habitat.

Fourth, it will also be valuable to report all the metrics usually associated with traditional definitions of "fallback," including time to and direction of initial movement following tagging. The timing and direction of initial movements can aid in interpreting behaviors. For example, chinook salmon (*Oncorhynchus tshawytscha*) were classified as "motivated" or "hesitant" based on the initial direction of movement following release (Bernard et al., 1999). Immediate upstream movement may indicate that the urge to spawn overrides other considerations. Immediate downstream movement may indicate altered migratory behavior (Olney et al., 2006). Fifth, distance, duration, and speed of movements following release should be reported. These metrics are often recorded in telemetry studies, but "normal" distances and times have not been identified. As examples, American shad

with limited upstream movement within 72 h were classified as "non-viable" (Sprankle, 2005), and sea lamprey (*Petromyzon marinus*) with brief upstream forays (<1 km) punctuated by long stationary periods (several weeks) were termed "atypical" (Andrade et al., 2007). In order to best interpret whether these movements were aberrant, more information is needed on patterns and mechanisms associated with pre-spawning fish behavior.

Sixth, if fish move downstream and then later return upstream, the time required to return to the tagging location should be documented. Often, as in our study, emphasis is placed on the upstream migration, and receivers are distributed upstream of the release location. However, this can limit a researcher's ability to assess and document downstream behaviors, whether normal or abnormal. If field interpretation of the tag effect depends on downstream movement, future telemetry studies should allocate receivers specifically to quantify downstream behavior. Seventh, the occurrence of short distance forays (<2 km) also should be reported, as this indicates active swimming behavior. The timing of these movements may indicate exploration (Keefer et al., 2008), the drive to spawn (Acolas et al., 2004), or a reaction to the environment (Dodson et al., 1972). If possible, these post-tagging movements should be linked to known information about success of spawning.

Finally, authors should clearly define and justify their reasons for excluding "fallback" fish from analyses. Varying methods have been used to determine whether "fallback" fish will be included in data analyses including eventual return upstream (Beasley & Hightower, 2000; Moser et al., 2000; Hightower & Sparks, 2003; Bailey et al., 2004; Olney et al., 2006) or movement within a specified time period (Chappelear & Cooke, 1994). The majority of alosine telemetry literature include fish in the analyses that eventually resume upstream migration after initial downstream movements. However, the criterion of limited upstream movement following tagging has also been used to exclude fish from analyses (Sprankle, 2005) and to identify altered migratory behavior (Olney et al., 2006). Researchers should report whether the entirety of the telemetry record is used, or if data are only collected once a fish resumes migration or moves a specified distance upstream (Bernard et al., 1999; Beasley & Hightower, 2000; Keefer et al., 2004). If researchers provide information on all of these parameters in future telemetry field studies, a body of literature will emerge on which to base tagging protocols, and from which much can be learned about spawning behavior in the field.

The high variability in downstream movement metrics has resulted in inconsistent interpretations of these movements. In the alosine telemetry literature, there is no agreement regarding the role of sex, age, or timing on post-tagging downstream movements. Males may be more affected than females because of their smaller size (Moser et al., 2000) or females may be more sensitive to the handling process due to their higher condition factor (Acolas et al., 2004). Young or virgin spawners of either sex may be more affected than older or repeat spawners (Hightower & Sparks, 2003) or there may be no link between "fallback" behavior, sex (Bailey et al., 2004), and age (Olney et al., 2006). Researchers have suggested that later migrants may respond rather differently to tagging and handling than early migrants (Glebe & Leggett, 1981; Bailey et al., 2004; Sprankle, 2005), but no consensus exists.

Although "fallback" in the alosine literature is defined as unnatural downstream movement related to tag effect and handling, salmonid telemetry studies rarely link "fallback" to tag effects or handling (Bernard et al., 1999; Makinen et al. 2000; Holbrook et al., 2009). Often the downstream movements of upstream migrating salmon are described as a purposeful behavior in response to the environment, obstacles, or a mechanism of homing (Keefer et al., 2006). These complex behaviors include overshooting of natal systems (Naughton et al., 2006), exploratory movements (Keefer et al., 2008), seeking alternate routes, waiting for appropriate conditions (Thorstad et al., 2005; Holbrook et al., 2009), disorientation in certain hydraulic conditions (Naughton et al., 2006), being swept over dams (Matter & Sandford, 2003), or varying sensitivity in distinct migratory phases (Makinen et al., 2000; Jokikokko, 2002). Aberrant movement in salmonids has not been explicitly related to "fallback" or tag effect (Young et al., 2006); for example, when radio tags were used to examine the effect of catch-and-release on adult Atlantic salmon (*Salmo salar*), uncharacteristic up and downstream movements of radiotagged fish observed post-release were attributed to angling (Thorstad et al., 2003). This marked difference in how "fallback" behavior is

interpreted across fish taxa may be because little is understood about the migrations of non-salmonid anadromous fishes. As the body of telemetry literature on other anadromous species grows, we anticipate the emergence of alternative hypotheses to explain the range of upstream and downstream movements in alosines.

Downstream movements post-tagging should be viewed on a continuum of potential consequences. "Fallback" may result in increased likelihood of injury or death during downstream movement, potential re-exposure to a fishery, reduced likelihood of reaching spawning grounds, migratory delay, and energy expenditure to re-gain lost ground (Bernard et al., 1999; Boggs et al., 2004; Scruton et al., 2007). From a management perspective, "fallback" may also result in inflated fishway counts (Naughton et al., 2006) or incorrect estimates of exploitation and fishing mortality rates (Olney et al., 2006). Migration abandonment is a severe consequence of "fallback," in which fish never resume upstream migration following "fallback" (Hightower & Sparks, 2003; Olney et al., 2006). However, as we have suggested, downstream movements following tagging need not be abnormal or have adverse consequences. Neither "fallback" nor abandonment precludes the possibility of spawning (Beasley & Hightower, 2000) if fish can use secondary spawning habitats (Acolas et al., 2004; Jepsen et al., 2005; Lopez et al., 2007; Maes et al., 2008). Furthermore, up and downstream movements may be part of normal pre-spawning migration, exploration, and habitat selection.

The trajectories of tagged alewives we used here to illustrate the range of possible movements would not be instructive if these fish movements were caused by tagging. We took exceptional care tagging our fish and used a detailed protocol that involved a limited number of designated taggers and several training sessions before the actual tagging. Increased plasma cortisol is part of a fish's primary response to stress, and the magnitude of corticosteroid response typically indicates the severity of the stressor (Barton & Iwama, 1991). Secondary responses to stress include changes in plasma glucose and the major ions, sodium and chloride (Close et al., 2003). The tagged fish held 24 h in our experiment did not exhibit significant differences in plasma cortisol, glucose, or chlorides relative to untagged fish held for this period. Handling and holding fish, whether associated with tagging or not, however, resulted in higher plasma cortisol and glucose and lower plasma chloride compared to initial levels of unheld fish. However, cortisol, glucose, and chloride levels of our anadromous alewives were not extreme. In a related study that transported anadromous alewives for 2 h, cortisol and glucose were much higher and chlorides much lower than the fish that were handled and held but not transported in this study [transported means: cortisol = 1047 ng/ml; glucose = 14.5 mM; chlorides = 55.1 mM (Frank, 2009); untransported means, (tagged and untagged combined): cortisol = 512.4 ng/ml; glucose = 9.9 mM; chlorides = 69.1 mM (this study)]. Thus, this lack of a difference between tagged and untagged alewives was not because both groups of fish were maximally stressed. Quantifying how tagging affects fish in the wild is a challenge because it is very difficult to measure fish behavior, physiology, or stress in the field without either tagging them or holding them in confinement. Stress related to handling occurs in virtually all animals in the wild, making this problem an inherent difficulty in studies of the behavior and physiology of wild animals. Certainly a tag may affect other aspects of fish performance (e.g., swim speed, searching behavior, depth in water column) besides what we measured. With advances in technology such as tags that can assess physiological condition, future researchers may be able to more precisely separate out tagging, handling, and confinement stress. With the increasing number of research studies on telemetry, understanding these physiological and behavioral tag effects in the field is both a critically important and extremely challenging area in which future research is needed.

Conclusion

In summary, we encourage other researchers to report the following data relative to post-tagging movements: the number of fish that move downstream; context of capture; time to initial movements; direction of and time to initial movements; characteristics of movements from the release site including distance, speed and duration at each location; changes in direction and associated distance, duration, and speed; and whether or not all fish are included in the analysis. Information on sex, age, and migration timing related to the incidence of "fallback" and other movements

will also be useful to better understand which fish are more likely to exhibit this behavior. Physiological assessments combined with behavioral studies will provide better information on how stressors, both human and natural, affect migratory behavior. With this information, we can start to sort out the complicated behaviors seen in most fish telemetry studies including river herring and other alosines.

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