Aquat Ecol (2014) 48:23–33
DOI 10.1007/s10452-013-9463-y

The fate of dead fish tagged with biotelemetry transmitters in an urban stream

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Received: 7 July 2013 / Accepted: 21 October 2013 / Published online: 13 December 2013
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Abstract Mortality is a key factor in understanding the population dynamics of fish. For studies using biotelemetry, missing individuals pose a challenge since the ultimate fate of both the animal and the tag are unknown. In this study, we document three releases of carcasses in a simulated small-scale summer fish kill in a small urban stream using juvenile white sucker (*Catostomus commersonii*). Passive integrated transponder (PIT) and radio tags were affixed to carcasses that were tracked to determine the fate of both the dead fish and the tags. Mean daily dispersal distances ranged from 0.0 to 7.6 m day^{-1} and included downstream and lateral dispersal. Of the 44 radio-tagged carcasses, 26 tags (and presumably carcasses) were consumed by scavengers; the majority were consumed by snapping turtles (*Chelydra serpentina*) with fewer carcasses scavenged by great blue heron (*Ardea herodias*), raccoon (*Procyon lotor*) and muskrat (*Ondatra zibethicus*). We also contrasted the decomposition rates of in-stream carcasses with those experimentally placed on the riverbank and found that while there was no significant difference in the time to carcass evisceration, the rate of decomposition was more rapid in-stream compared to on-shore. Radio tag loss during the decomposition study was moderate (one of three lost); PIT tag loss occurred when carcasses became eviscerated, typically by invertebrates. By examining the role of scavengers, dispersal and decomposition, it is possible to understand the fate of dead fish, the fate of tags and role of mortality in tagging experiments and the connections between stream and riparian habitats and organisms. This information will help inform the interpretation of potential mortalities in fish tracking studies and improve fish kill investigations.

Keywords PIT tag · Radio telemetry · Urban stream · Fish kill · Mortality · Scavengers

Handling Editor: Thomas Mehner.

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Introduction

Mortality is important for understanding population dynamics, making it the cornerstone of fish population and management models (Beverton and Holt 1957; Ricker 1975). Total mortality in exploited fish populations is a combination of natural mortality (e.g., old age, disease, predation, starvation, winterkill) and

fishing mortality (either direct harvest or discard and release mortality). In both exploited and unexploited populations, mortality can also be associated with other non-harvest anthropogenic activities such as pollution, turbine entrainment and cold shock (Pauly 1980; Kerns et al. 2012). Direct estimates of the natural mortality rate of fish are difficult to obtain because of the lack of direct information about natural deaths (Vetter 1988; Pascual and Iribarne 1993). To estimate the instantaneous natural mortality rate, it is possible to use various techniques, including tag return methods and more recently telemetry methods (Vetter 1988; Quinn and Deriso 1999; Hightower et al. 2001; Xiao 2001; Pollock et al. 2004). Fishing mortality, at least the harvested component, is comparatively easy to measure; however, the discard mortality component of fishing mortality is more difficult to quantify because it tends to happen after release (Davis 2010; O'Toole et al. 2010). Most other sources of anthropogenic mortality are documented by direct observation (e.g., counting fish removed from entrainment screens or counting fish during fish kill investigations after a pollution event; Labay and Buzan 1999; King and O'Connor 2007).

At an individual level, there has been little research on the fate of fish carcasses (Schneider 1998; La and Cooke 2011). Such information could improve our ability to document natural and anthropogenically induced mortality; it could also address practical issues associated with fish kill investigations (Hill 1983; Labay and Buzan 1999) or telemetry studies, where it is necessary to determine whether and when fish die (e.g., Cooke et al. 2006; Donaldson et al. 2008). The reality is that even in the presence of high mortality events (e.g., Cooke et al. 2004), it is seldom that dead fish are observed, except perhaps in the case of fish kills in discrete locations during periods which coincide with human presence (Hill 1983; La and Cooke 2011). Presumably carcasses are scavenged or decompose, although whether that happens at the site of death or elsewhere is unclear. Ryon et al. (2000) simulated a fish kill in a small stream system and noted that basic surveys for carcasses were effective if conducted directly after the event; however, they noted substantial carcass removal by scavengers and associated carcass dispersal, especially within the first 24 h. In the absence of scavengers, decomposition starts inside the body, progressing through tougher tissues and bones, with some remnants of the carcasses of adult rainbow trout (*Oncorhynchus mykiss*) lasting between 50 and 120 days depending on water temperatures (Minshall et al. 1991). In general, knowledge of the roles of scavenging, dispersal and decomposition on individual carcasses is poor.

Although fish death can and does occur in all types of water bodies, there are particular challenges in freshwater lotic systems. Once fish die in streams or rivers, carcasses can be dispersed downstream without the aid of scavengers. Ryon et al. (2000) noted some limited downstream dispersal (typically <35 m) as a result of flow. Patterson et al. (2007) noted that water temperature was inversely correlated to the number of days required for sockeye salmon (*Oncorhynchus nerka*) carcasses to float to the surface of the water, making it difficult to detect carcasses in rivers; detection was further confounded by the turbidity of the water. In general, it is believed that discharge influences dispersal distances in lotic waters, whereas fish carcasses in lentic waters are prone to high scavenging rates and decomposition and thus usually go unobserved (Schneider 1998). Regardless of the system, carcasses can also be exposed to terrestrial scavengers and aerial decomposition as a result of low water conditions, further complicating any assessment of carcass fate in an aquatic environment.

From a biotelemetry perspective, 'mortality sensors' have been developed to change their signal when a tag has been stationary for a predetermined period of time that is presumed to indicate the death of the tagged individual (Cooke et al. 2012). Carcasses (and their associated tags) that are consumed either through predation or scavenging may not exhibit this sedentary period and therefore may still appear alive (Cooke et al. 2013). A researcher may then continue to track the tag, erroneously assuming that they are tracking a living fish. It is therefore important to determine the fate of the tag as well as the fate of the carcass so that the ultimate fate of each individual can be accounted for, whether they have left the study area, were preyed upon or died as a result of disease or other factors.

The overall goal of this study was to improve our knowledge of the fate of dead fish in a small urban stream and included three specific objectives. The first objective was to simulate a small-scale fish kill and use passive integrated transponder (PIT; commonly used to identify individuals) tags and radio tags to track the dispersal and fate of dead fish released into a stream.

The second objective was to contrast the decomposition rates of deceased fish in-stream with those on the riverbank in cages that exclude large scavengers. The final objective was to identify the ultimate fate of the electronic tags both during dispersal and decomposition. Based on previous studies, we broadly hypothesize that carcasses will move downstream and either shed their tags due to decomposition or be consumed by scavengers.

Materials and methods

Study area

The study was conducted in Watts Creek in the Kanata region of the municipality of Ottawa in southeastern Ontario. The total drainage area is approximately 24.9 km^2 with a change in elevation of 45 m from the headwaters to its connection with the Ottawa River. Watts Creek is a fourth-order creek prior to Kizell Drain joining the system. The dominant substrates are silt and clay, with the exception of sections that are adjacent to the Canadian National Railway train track where cobble was added during construction and sections where riffles occur in upstream areas of Watts Creek.

During the study period, Watts Creek was devoid of any in-stream vegetation in the segment where Release 1 (R1) and Release 3 (R3) were carried out; during Release 2 (R2), patchy areas of in-stream vegetation were present (e.g., *Elodea canadensis, Cladophora* spp.). During peak flow after a rainfall event, water discharge as high as 1.2 $m^3\ s^{-1}$ has been recorded; however, mean discharge is typically below 0.17 $m^3\ s^{-1}$, and the stream gradient is low (JL Richards and Associates Limited 1976).

Through a seasonal study of the fish community in Watts Creek, it has been determined that the system naturally has a low density of fish (annual average of 66 fish per 100 m transect; Shireen Bliss, personal communication, 14 April 2013). Fishes found in the creek in order of abundance include banded killifish (*Fundulus diaphanous*), central mudminnow (*Umbra limi*), longnose dace (*Rhinichthys cataractae*), brook stickleback (*Culaea inconstans*), creek chub (*Semotilus atromaculatus*) and white sucker (*Catostomus commersonii*). Potential scavengers include crayfish (*Orconectes* spp.), great blue herons (*Ardea herodias*) and snapping turtles (*Chelydra serpentina*); no fishes known to be scavengers have been found in this system (Shireen Bliss, personal communication, 14 April 2013). Tracks and evidence of raccoons (*Procyon lotor*), muskrats (*Ondatra zibethicus*) and coyotes (*Canis latrans*) have also been seen in the Watts Creek area.

Table 1 Mean total length and weight of white suckers (*Catostomus commersonnii*) for each release round

Release round	Mean total length, mm (SD)	Mean weight, g (SD)	Sample size, *n*
1	127 (11)	19.2 (5.7)	21
2	140 (12)	23.2 (5.9)	14
3	140 (15)	29.6 (6.3)	9

While carcasses in R1 were significantly shorter than those in R2 and R3 and carcasses in R1 and R2 were significantly heavier than carcasses in R3, all individuals were still categorized as juveniles (Beamish 1973)

Dispersal study

In August 2012, there were three separate releases of fish carcasses into Watts Creek to simulate mortality events. White sucker were selected as the test species for this study because it is a common species found in Watts Creek and is readily available at local bait shops. Moreover, white sucker are widely distributed in eastern and mid-western North America with confamilials throughout North America. Release 1 (R1; 8 August 2012, $n = 21$; Table 1) was of a high density (one carcass released every 5 m), which is indicative of an anthropogenically induced fish kill event (e.g., Kennedy et al. 2012) such as point source pollution from a water treatment facility or pulp and paper mill. Releases 2 (R2; 10 August 2012, $n = 14$; Table 1) and 3 (R3; 20 August 2012, $n = 9$; Table 1) were of a lower density (one carcass released every 50 m), which is characteristic of a natural mortality event such as disease (Wood 1960). Further justification for changes in spacing of fish releases was that during R1, the majority of carcasses were consumed by a single scavenger within 24 h (see 'Results'); therefore, carcasses in subsequent releases were placed at greater spatial intervals. Live fish were acquired from a local bait shop within 24 h prior to release into the system. Fish were transported to the laboratory and/or the study site in a cooler with aerated water and euthanized within 2 h prior to release. Fish were euthanized

Table 2 Condition index scores (CIS) and condition descriptions of fish carcasses that were evaluated for the decomposition study

CIS	Condition description
1	Carcass appears in excellent condition, no decay
2	Carcass appears in good condition, some decay, fins are frayed, minor scale loss
3	Carcass appears in poor condition, evisceration has occurred, advanced decay, oculi removed, scale loss
4	Carcass appears to be in very poor condition, evisceration has occurred, oculi removed, advanced decay, disarticulation, major scale loss
5	Carcass appears to be in poorest condition, evisceration has occurred, oculi removed, very advanced decay, very advanced disarticulation, only remains present

Condition descriptions were adapted from Gende et al. (2002)

using cerebral percussion followed by spinal severance.

Fish for R1 were transported to the laboratory to be measured, weighed (Ohaus Scout II Top Loading Balance) and tagged with a 23 mm HDX PIT tag (Oregon RFID, Oregon, USA), which was inserted into the peritoneal cavity using an injector needle. Fish were euthanized within 2 h prior to release, and a radio telemetry tag (Model BD-2, 1.2 g, 3.5 mm × 8 mm with a 16-mm antenna; Holohil Ltd, Carp, Ontario; lifespan range of 43–74 days) was attached mid-dorsally using braided fishing line (Shimano PowerPro, Super Slick, 7 kg). An anchor tag was attached to the dorsal fin using a tagging gun to ensure that carcasses could be identified even if both the PIT and radio tags were lost. Fish used for R2 and R3 were transported to the study site and were immediately euthanized, measured, weighed and tagged in the same manner as R1 fish.

All fish were released into the thalweg of Watts Creek. For R1, releases of fish carcasses were done at 5-m intervals in contrast to the 50-m intervals used for both R2 and R3. At each location of release, a wooden stake was driven into the bank and flow velocity (m s^{-1} at 50 % depth; FP111 Global Water Flow Probe) and depth (cm) were recorded in the thalweg. Fish were tracked twice daily with a hand-held radio receiver (Biotracker, Lotek Wireless Inc., Newmarket, Ontario, Canada), and a three-element Yagi antenna until the fish carcass reached a condition index score (CIS) of 5 (Table 2, 1 = excellent condition, 2 = good condition, 3 = poor condition, 4 = very poor condition, 5 = poorest condition; adapted from Gende et al. 2002) was consumed by a scavenger or when dispersal had not occurred for 5 days. When a fish carcass was located, the flow velocity (m s^{-1} at 50 % depth) and depth (cm) at the carcass location were recorded and the CIS was assigned to describe the decay of the carcass. Dispersal was measured as the shortest straight-line distance within the confines of the creek between the point of release and the carcass location. Due to variability in the duration of tracking for each release round, these values were converted to m day^{-1} to allow for comparison among R1, R2 and R3. Photographs of the carcasses were taken, and the presence or absence of the radio and PIT tag (using a pocket reader, Oregon RFID, Oregon, USA) was noted.

Decomposition study

Twenty white suckers were acquired from a bait shop on 20 August 2012. Fish were transported to the laboratory in an aerated cooler of water, and all individuals were measured and weighed. Twelve individuals were tagged with PIT tags in the same manner as in the release study. After tagging, each fish was killed, and three randomly selected fish were tagged with a radio tag in the same manner as in the release study. Each individual was placed into a sealed trap made of plastic mesh (Quest, 1.5 × 1.5 cm mesh size). These traps were attached to a T-bar in groups of two or three cages. A total of seven sites were selected: four in-stream sites were chosen located in pools spaced along the release area for R1; three of these were paired with on-shore sites that were in the riparian zone within 5 m of the in-stream site. Fish carcasses were assessed and photographed daily for 13 days and then on five occasions over a period of 18 days. A CIS was assigned to describe the decay of the carcass. Water temperature data were obtained from thermal loggers that were situated within 1.2 km of the in-stream sites. Air temperature and precipitation data were acquired from an Environment Canada weather reporting station (45°23′00.000″N, 75°43′00.000″W, elevation 79.20 m) approximately 14 km from the study site.

Statistical analysis

An analysis of variance (ANOVA) was performed to test whether there were significant differences in total length and weight of carcasses among release rounds

and in the mean daily dispersal rates among release rounds. A post hoc Tukey's HSD test was performed when the ANOVA was significant. Evisceration data did not meet the assumptions of an ANOVA; therefore, a nonparametric Wilcoxon test was used to determine whether there were significant differences between time to carcass evisceration on-shore and in-stream. A bivariate linear regression of condition and day of year by location (on-shore, in-stream) was performed, and decomposition rate was determined as the slope of this line. All tests were conducted in JMP 9.0 statistical software (Copyright© SAS Institute, Cary, NC, USA), and statistical significance was assessed at $\alpha = 0.05$.

Results

Fish dispersal

There were significant differences in the total lengths of suckers between release rounds (Table 1; ANOVA, $F = 6.877$, $P = 0.03$, $DF = 2$). Suckers in R1 were significantly smaller than those in R2 (Tukey's HSD, $P = 0.007$, SE = 4.13) and R3 (Tukey's HSD, $P = 0.019$, SE = 4.77). There were also significant differences in the weights of suckers between release rounds (Table 1; ANOVA, $F = 9.786$, $DF = 2$, $P = 0.0003$), such that suckers in R3 were significantly heavier than those in R1 (Tukey's HSD, $P = 0.0002$) and R2 (Tukey's HSD, $P = 0.041$).

Due to high scavenging rates, fish carcasses were tracked for different time periods during the release rounds such that carcasses were tracked for an average 6.5 days (SD = 0.7, $n = 8$) and 2.6 days (SD = 1.6, $n = 7$) for R2 and R3, respectively, and for only 1 day during R1. All carcasses were located either on the bottom of the stream bed or suspended on algal mats and macrophytes; none of the carcasses were located near the surface of the stream. Excluding individuals after they were consumed by a scavenger, there was no significant difference in mean daily dispersal distance for R1 (1.2 ± 1.2 m day^{-1}; median = 0.8 m day^{-1}, $n = 3$), R2 (1.6 ± 2.7 m day^{-1}; median = 0.4 m day^{-1}, $n = 8$) and R3 (1.0 ± 1.9 m day^{-1}; median = 0.7 m day^{-1}, $n = 7$; ANOVA, $F = 0.2315$, $DF = 2$, $P = 0.796$).

Scavenging rates were highest in R1 where 86 % of carcasses were consumed by a single snapping turtle within 24 h of the release (Table 3). Carcasses in R2 and R3 were scavenged more sporadically during the day and night throughout the study period, but ultimately 50 and 33 % were scavenged in R2 and R3, respectively (Table 3). A single snapping turtle was responsible for the majority of scavenging in R2 (6 of 7 carcasses) with a muskrat taking the last individual. For R3, a great blue heron consumed two tagged fish and a raccoon took one other. We continued to track carcasses that were consumed by scavengers in an attempt to determine the fate of the electronic tags post-consumption, but in all instances, the scavenger either left the study area or the radio tag stopped functioning before it could be recovered.

Table 3 The fate of dispersed carcasses in each release round

Release round	Number of carcasses	Ultimate fate of carcasses
1	18	Preyed on (snapping turtle)
1	2	Decomposed
1	1	Radio tag battery died
2	7	Decomposed
2	6	Preyed on (snapping turtle)
2	1	Preyed on (muskrat)
3	5	Decomposed
3	1	Preyed on (raccoon)
3	1	Preyed on (heron)
3	1	Likely preyed on (heron)
3	1	Unknown

Mean flow velocity measured during surveys was significantly different among all three rounds (ANOVA, $F = 23.2$, $DF = 2$, $P < 0.0001$) with the highest velocities occurring in R1 (0.2 ± 0.1 m s^{-1}, $n = 9$), followed by R2 (0.1 ± 0.1 m s^{-1}, $n = 83$) and R3 (0.0 ± 0.0 m s^{-1}, $n = 35$). Mean depth in R1 (19.9 ± 10.7 cm, $n = 9$) was significantly greater than in R3 (17.6 ± 7.3 cm, $n = 35$; ANOVA, $F = 6.216$, $DF = 2$, $P = 0.003$; Tukey's HSD, $P = 0.003$), while depths during R2 were the deepest (23.9 ± 9.5 cm, $n = 83$). According to precipitation data from the Environment Canada weather reporting station, there were two rain events (>0.2 mm) during R1 totaling 14.5 mm (14.5 mm day^{-1}), six rain events during R2 totaling 35.2 mm (5.4 mm day^{-1}) and two rain events during R3 totaling 0.4 mm (0.2 mm day^{-1}).

Decomposition study

Three carcasses from the on-shore treatment were preyed upon, as cages were found ripped open but no

tracks or other evidence of the scavenger were observed. There was no significant difference in time to evisceration (Wilcoxon, $\chi^2 = 2.1008$, $DF = 1$, $P = 0.147$) between carcasses on-shore (52.3 ± 19.5 h, $n = 6$) and those in-stream (84.8 ± 49.8 h, $n = 11$). However, the rate of decomposition (CIS day^{-1}) was slower on-shore (0.20, $R^2 = 0.45$, 74 observations of 7 individuals) than in-stream (0.35, $R^2 = 0.79$, 137 observations of 12 individuals). The on-shore decomposition rate decreased (0.07, $R^2 = 0.25$, 94 observations of $n = 7$) when individuals that became mummified after 42 days were included in the analysis (Fig. 1a). One of the three radio tags used for this study was detached from the carcass; this occurred after 7 days when the carcass became disarticulated. In contrast, PIT tag loss occurred in all cases when the carcasses became eviscerated (Fig. 1b; mean time to evisceration when in-stream and on-shore carcasses were combined was 73.3 ± 43.9 h, $n = 17$).

The mean water temperature during the study was 17.4 °C (SD = 2.5, $n = 66$), according to data obtained from thermal loggers situated within 1.2 km of the in-stream decomposition sites. The mean air temperature during the study was 18.5 °C (SD = 4.0, $n = 33$) and mean daily precipitation was 4.1 mm (SD = 8.1, $n = 33$), according to data obtained from the Environment Canada weather reporting station approximately 14 km from the study area.

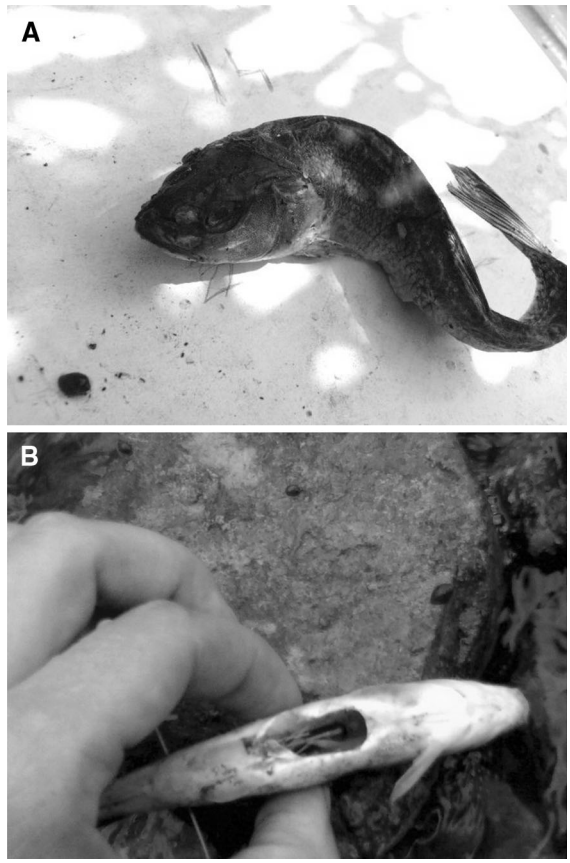

Fig. 1 *Top image* **a** is of a mummified juvenile white sucker from the decomposition study. Mummification occurred only at the on-shore site and effectively ceased the decomposition process. *Bottom image* **b** an eviscerated juvenile white sucker (*Catostomus commersonnii*) with a PIT tag in the abdominal cavity

Discussion

This small-scale fish kill study demonstrated that carcasses are either quickly consumed by scavengers or decompose, making the identification of small-scale fish kills challenging if not investigated promptly. Additionally, these results support the need to recognize the role of scavengers, as they make it difficult to detect dead fish (La and Cooke 2011). The majority of the fish released into the system were scavenged (59 %), with snapping turtles consuming most of the carcasses (24 of 28). We attribute the differential rates of scavenging among the three release rounds to the distances between the carcasses at the time of release although it is also presumably linked to scavenger density and behavior. In the first release, a snapping turtle consumed 18 of 21 carcasses <24 h post-release. The close proximity of the carcasses (i.e., 5 m separation between carcasses) presumably allowed the snapping turtle to locate and consume the carcasses as it moved upstream, although three of the carcasses along the dispersal path were not consumed. In contrast, following R2 (with carcasses spaced at 50-m intervals), a different snapping turtle consumed six carcasses over 7 days. In both instances, the snapping turtles were tracked for at least 7 days after tag ingestion, and the radio tags were not excreted before the radio signals were lost. Since the radio tag signals were not encountered over the remainder of the study period, it is possible that the turtles' stomach acid destroyed the transmitters. Snapping turtles are known to have a fast digestive turnover time (31 h; Parmenter 1981) at 25 °C; however, as these results

are for tissue, we would expect longer digestive turnover rates for radio tags. The radio tag may not have been detected if the snapping turtle left the study area, which is possible since snapping turtles are known to have large home ranges in the late summer post-nesting (Paterson et al. 2012). The minimum lifespan of the radio tags used in this study was 43 days so it is unlikely that tags failed during the study period, following ingestion by the snapping turtle. Although it is not clear why the radio tag signal was lost, controlled tag life studies to address premature tag failure and correct survival estimates are useful when mortality must be accounted for (Townsend et al. 2006; Beeman et al. 2010).

Scavengers such as heron, raccoon and muskrat were also found to consume carcasses in R2 and R3. Live fish are the most common food item for great blue heron, but on occasion, they do eat dead fish (Butler 1997). Direct observation of scavenging by heron was observed in one instance when a heron was tracked to a tree 120 m away from the stream. In the second instance, heron tracks were used to identify the scavenger. No direct observations were made of the raccoon and muskrat; however, one tag was tracked into a muskrat burrow, and raccoon tracks were found next to another. While muskrat primarily consume vegetation (Lacki et al. 1990), they are omnivorous and have been previously observed to eat both live and dead fish (Willner et al. 1975). Raccoons are a known scavenger of dead fish (Schoonover and Marshall 1951). Two carcasses were also presumed to have been dispersed by unknown scavengers since they were found upstream; however, no tracks or evidence of the identity of the scavenger(s) was found. In addition to larger scavengers, leeches (*Hirudo* spp.), snails (*Helix* spp.) and various unidentified benthic invertebrates were often seen on the carcasses (data not shown); scavenging by crayfish (*Cambarus* spp.) is presumed as exoskeletons were frequently found near carcasses and crayfish are known scavengers of dead fish (Willman et al. 1994).

The rapid removal of carcasses by scavengers is consistent with Ryon et al. (2000), who found that carcasses were quickly removed from a stream system such that 40–90 % fewer carcasses were found after 24 h. In this study, carcasses were removed by scavengers more completely and quickly when carcasses were available in higher densities (R1 vs. R2 and R3). While this may suggest that high-density fish kills might be more challenging to identify, it is important to note that smaller-scale die-offs will be equally challenging to identify given the dispersed nature of the carcasses. Regardless, we deem it important to reiterate the findings of Ryon et al. (2000) that prompt discovery of fish kills is essential to fully quantify the extent of the die-off.

Despite significant differences in velocity, which were likely caused by higher rainfall in R1 relative to R2 and R2 relative to R3, there were no significant differences in the mean daily dispersal distances among release rounds. Furthermore, although we hypothesized that downstream dispersal would occur, our observed dispersal rates were quite low relative to those seen in a system with similar flow conditions (Ryon et al. 2000). We attribute these differences in part to our methods of inserting PIT tags and attaching the radio tags and caution against using the dispersal distances noted in this study to extrapolate for natural fish populations. The insertion of the PIT tag resulted in an opening into the peritoneal cavity, and the placement of the radio tag likely ruptured the swim bladder in most individuals. These factors would have resulted in a specific gravity greater than one, thus preventing the carcass from surfacing (Patterson et al. 2007). In addition, while we did not specifically evaluate the effect of macrophytes on limiting dispersal, some carcasses were found to be suspended mid-water column in vegetation (e.g., *E. canadensis*). These patches of aquatic vegetation were predominantly found during R2 and may have reduced the dispersal rate during this release for some individual carcasses.

While our study only focused on releases during low-flow conditions, in a similar study, where fish were released intact under comparable flow conditions, the majority of carcasses did not disperse beyond 35 m; however, under high-flow conditions, almost all individual carcasses dispersed greater than 35 m downstream within 24 h. The maximum dispersal distance between experiments increased from 345 m to 585 m with a fivefold increase in stream discharge (Ryon et al. 2000). In a study that monitored fish behavior, route-specific passage and route-specific survival through dam (Beeman et al. 2010), the carcass of a yearling salmonid was found to have dispersed 29 km downstream. This study was done on a large river, where the mean daily total discharge was 3,160 m^3 s^{-1}. Comparatively, estimated discharge in

Watts Creek was 0.39 m^3 s^{-1} during the study period (Shireen Bliss, personal communication, 15 August 2012). Therefore, it is possible that our limited dispersal distances are more linked to low-flow conditions than the piercing of the peritoneal cavity and the rupturing of the swim bladder; however, we cannot differentiate between these two possibilities. The dispersal distances observed in this study are therefore likely only applicable to similar, small low-flow systems, and we caution against their general application to other lotic systems at this time.

The role of vertebrates in the global and regional transport and release of nutrients are well recognized (Schindler et al. 2005), and the decomposition of fish carcasses can be an important source of nutrients (Chidami and Amyot 2008). In salmonids, the presence of the carcasses in streams can stimulate bacterial and fungal activity, contributing to nutrient recycling and maintenance of fertile nursery areas for fish (Richey et al. 1975). While we found no difference in the time to evisceration of carcasses on-shore compared to in-stream, the overall rate of decomposition was slower. Studies of fish decomposition in other systems (e.g., Kitchell et al. 1975; Parmenter and Lamarra 1991; Schneider 1998) have shown that decomposition rates are closely related to temperature and fish size. However, despite higher temperatures in the air than in the water, we observed slower rates of decomposition. This may be explained by the facilitation of in-stream decomposition by scavenging and bacterial degradation because carcasses are typically not buried under the sediment following death (Chidami and Amyot 2008). The exclusion of large scavengers, which may have the ability to take the entire carcass, both on-shore and in-stream allowed us to study the decomposition that resulted from the assemblage of small scavengers (e.g., leeches, snails, crayfish) and microbial decomposition.

The on-shore decomposition rate decreased when carcasses that did not decompose at the end of the study period were included. Mummification likely occurred as a result of exposure to sunlight and exclusion of large scavengers. Three of the four mummified individuals were located at the same site, which was exposed to sunlight due to a lack of surrounding vegetation. The other carcass was located at a different site and may have become mummified due to its orientation among the other cages, which resulted in relatively higher sun exposure compared to the other two cages at the site.

In the dispersal study, radio tag loss did not occur until the carcass was decomposed to a CIS of 5 or consumed by a scavenger. As hypothesized, PIT tag loss occurred when carcasses became eviscerated, but the tags were often found in the empty body cavity of the carcass, in which case the tag could be recovered. Based on this assessment, it appears that external tagging approaches, such as those used for the radio tags, are more likely to remain with the carcass than internal tags. This suggests that external tagging may be preferable for tracking studies where significant mortality may be anticipated (e.g., a catch-and-release or bycatch study; Donaldson et al. 2008).

Radio tag loss in the decomposition study was moderate, with only one of three radio tags becoming detached from the carcasses, but similar to the dispersal study, loss occurred when the carcass became disarticulated. Retention of the PIT tag in decomposing individuals was found to be low since decomposition appears to progress from inside the carcass toward the skin (Minshall et al. 1991; Stevenson and Childers 2004). As in the dispersal study, PIT tag loss occurred when carcasses became eviscerated, and when tags were found in the carcass cavity, the tag could be recovered. PIT tags were found inside the body cavity more frequently in the decomposition study, likely due to the restricted movement of the carcasses. Three carcasses were preyed upon during the study as cages were found ripped open, but no tracks or other evidence of the scavenger was seen.

Although we tried to use similar-sized carcasses for the study, white suckers in R1 were significantly smaller than those in R2 and R3 and white suckers in R3 were significantly heavier than those in R1 and R2. Despite the differences in size, all individuals would still be considered 'juveniles' given the natural variability in weight and length within white sucker age classes (Beamish 1973). Since all individuals were juvenile white suckers of a similar age class, the observed size differences likely do not confound a comparison among the three releases especially since there were no observed differences in dispersal rates among the three rounds. That being said, we must acknowledge it is possible that the observed differences may have contributed to the higher rate of consumption of the smaller individuals in R1, since some predators are known to preferentially select for smaller fish (Juanes and Conover 1994).

Conclusion

Our findings demonstrate that a single scavenger can consume a large proportion of carcasses, especially if the carcass density is high, which supports our hypothesis, although we did not predict such high predation rates. Similar predation rates were seen in a study by Schneider (1998), where yellow bullheads (*Ameiurus natalis*) and turtles consumed 82 % of carcasses after a fish kill in a small lake. Much of the predation observed in our study occurred at night although tracking the carcasses twice daily allowed us to observe diurnal and nocturnal predation. The majority of turtle, raccoon and muskrat scavenging occurred at night, while heron scavenging occurred during the day. Tracking a scavenger after it has consumed a radio-tagged fish can occur unintentionally, especially when the scavenger is not seen and when the radio tag is not excreted. It would have been difficult to distinguish the scavenger movement from the movement of a live fish, especially if the scavenger is restricted to the aquatic system being studied. Since this study was not done using live fish and we directly observed several scavengers, we were able to determine the fate of the carcasses. Under most circumstances, however, applying telemetry methods to aquatic systems can be difficult because fish cannot be observed directly, so the fate of individuals (i.e., live vs. dead) is usually based on the movement (e.g., Thompson et al. 2007; Donaldson et al. 2008; Yergey et al. 2012).

Information on the fate of individuals can improve our ability to document both natural and anthropogenically induced mortality, which is an important factor in population dynamics (Hueter et al. 2006), and can address practical issues related to fish kills or telemetry studies. La and Cooke (2011) discuss key challenges that must be overcome in order to improve fish kill investigations and suggest a standardized database for reporting fish kills. Information such as the number of species affected and the size of fish affected will help standardize reporting and establish 'causation'. Although it cannot be assumed that the presence of carcasses indicates that fish died within the immediate vicinity, it is possible to establish basic dispersal patterns in lotic systems with similar flow regimes to discern the source of the pollutants (Ryon et al. 2000). Studies similar to the current study but in larger and higher velocity systems would be beneficial in providing information on the fate of individuals and basic dispersal patterns. Importantly, this study documented the inherent connectivity between the stream and riparian habitat and organisms, emphasizing the role of dead fish in providing food for semi-aquatic and terrestrial animals as well as the role of those animals in structuring energy dynamics in stream ecosystems.

Acknowledgments Robert Lennox, Beverly Allan, Alyssa Cousineau, Lauren Stoot, Jacqueline Chapman, Maja Cvetkovic and Shannon Bower provided intellectual and field support. Financial support was provided by the National Capital Commission (NCC) and the Natural Sciences and Engineering Research Council of Canada. Cooke is supported by the Canada Research Chair program.

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