

## Fish decomposition in boreal lakes and biogeochemical implications

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### Abstract

A field study in a boreal lake using a remotely operated vehicle equipped with a camera established that falling fish carcasses did not tend to be buried in sediments after deposition. Decomposition rates of fish carcasses in three boreal lakes were experimentally assessed at different depths. In shallow waters (between 0 and 4 m), decomposition was fast (half lives,  $\tau$ , ranging from 40 to 230 h) and controlled by vertebrates. In deep waters (below the thermocline), decomposition was slow ( $\tau$  between 770 and 1,733 h) and was controlled by bacterial processes. Water temperature was a promising predictor of decomposition half-lives in freshwater. Using a novel underwater infrared camera system, we identified the daily and seasonal patterns of scavenging activity by littoral fish. Only three species displayed scavenging behavior, with creek chubs being the most active. Fast fish-mediated littoral recycling of fish carcass may explain the lack of direct observations of carcasses in lakes. Estimates of phosphorus fluxes in one of the studied lakes indicate that falling carcasses can represent a significant water-to-sediment flux of nutrient.

Ecologists have long recognized the role played by vertebrates in the global and regional transport and release of nutrients (Schindler et al. 2005). More recently, their role in the transport of contaminants has emerged as a fruitful field of research in aquatic ecology (Blais 2005; Blais et al. 2007). This long-range biodelivery of pollutants and nutrients is expected to be especially significant for migratory animals, such as anadromous fish. In particular, the postmortem influence of Pacific salmon on the biogeochemical dynamics of receiving freshwater ecosystems has drawn much attention (e.g., Krümmel et al. 2003; Schindler et al. 2005; Fenoglio 2005). Recently, the role of arctic seabirds on contaminant cycling has also been documented (Blais et al. 2005).

Vertebrates can also influence nutrient cycling at the ecosystem scale. For instance, bears are known to transport salmon-derived nutrients from stream to land, with significant effects on the productivity of adjacent forested ecosystems (Helfield and Naiman 2006). Also, mobile avian scavengers breeding on islands in salmon nursery lakes can create hot spots of biological productivity by concentrating nutrients near their colonies (Payne and Moore 2006).

In lakes not affected by such massive mortality events, the role of vertebrate scavengers as vectors of nutrients is less understood. Although fish carcasses are rarely seen at

the bottom of lakes or on their shores, a number of studies on freshwater systems have reported that estimated natural mortality rates not due to predation are high, ranging between 10% and 67% per year (e.g., Craig 1984; Lorenzen 1996; Schneider 1998; Allen et al. 1998; Mills et al. 2002), with a mean of about 20–25% per year (Reznick et al. 2002). These falling carcasses constitute a water-to-sediment flux of biomass that could alter the cycling of nutrients (Parmenter and Lamarra 1991; Stevenson and Childers 2004) and bioaccumulative contaminants (Sarica et al. 2004).

The fate of fish carcasses after deposition at the sediment surface of lakes is poorly documented. Several articles on the fate of large fish and whale carcasses in the deep ocean floor have been published (e.g., Premke et al. 2003; Soltwedel et al. 2003; Ruxton and Houston 2004), but they are not directly applicable to lakes. Schneider (1998) conducted the only published experimental study on the fate of fish carcasses in a lake not subjected to massive fish mortality. Although the nonpredatory mortality rates of this population ranged from 25% to 40% per year, few carcasses could be found. Schneider (1998) concluded that, in this lake, this paradox could be partly explained by the unseen decomposition of fish carcasses in deep water and the ability of resident scavengers to keep up with the supply of dead fish. However, this study did not investigate the factors influencing the decomposition rates of carcasses.

The present study aims at testing some key hypotheses regarding fish decomposition in lakes in the absence of massive mortality events, to reach a better understanding of its effect on the cycling of matter. Our first hypothesis is that carcasses are not buried upon deposition and lie on sediments where they can be degraded by animals and bacteria. Such a burial would affect further degradation and likely lengthen the turnover time of nutrients in lakes.

Second, we investigate the relative importance of two modes of decomposition in lakes: bacterial decomposition and vertebrate scavenging. Bacterial decomposition will presumably lead to the complete mineralization of nutrients

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Table 1. Location, physical characteristics, and fish species (captured during the study) of the three lakes used in this study.

	Lake Triton	Lake Croche	Lake Cromwell
Location	45°59'15"N, 74°00'29"W	45°59'30"N, 74°00'50"W	45°59'20"N, 73°59'55"W
Area	0.02 km <sup>2</sup>	0.19 km <sup>2</sup>	0.11 km <sup>2</sup>
Volume	35,000 m <sup>3</sup>	877,000 m <sup>3</sup>	371,000 m <sup>3</sup>
Watershed area	0.2 km <sup>2</sup>	0.8 km <sup>2</sup>	9.9 km <sup>2</sup>
Maximal depth	4 m	11 m	9 m
Mean depth	2.1 m	4.8 m	3.6 m
Fish species	<i>Lepomis gibbosus</i> , pumpkinseed; <i>Phoxinus eos</i> , northern redbelly dace	<i>Lepomis gibbosus</i> , <i>Phoxinus eos</i> , <i>Semotilus atromaculatus</i> , creek chub; <i>Catostomus</i> <i>commersonni</i> , white sucker; <i>Semotilus corporalis</i> , fallfish; <i>Pimephales notatus</i> , bluntnose minnow; <i>Notropis rubellus</i> , rosyface shiner; <i>Richardsonius balteatus</i> , redside shiner; <i>Hybognathus</i> <i>hankinsoni</i> , brassy minnow; <i>Exoglossum maxillingua</i> , cutlips minnow; <i>Salvelinus namaycush</i> , lake trout; <i>Salvelinus fontinalis</i> , brook trout	<i>Lepomis gibbosus</i> , <i>Phoxinus eos</i> , <i>Semotilus atromaculatus</i> , <i>Catostomus commersonni</i> , <i>Semotilus corporalis</i> , <i>Pimephales</i> <i>notatus</i> , <i>Notropis rubellus</i> , <i>Richardsonius balteatus</i> , <i>Hybognathus hankinsoni</i> , <i>Exoglossum maxillingua</i> , <i>Ictalurus</i> <i>nebulosus</i> , brown bullhead
Other potential scavengers	Leeches, gull	Crayfish, turtles, gull	Leeches, crayfish, turtles, gull

and pollutants, which would then eventually re-enter the food web at its base. In contrast, vertebrate scavenging will promote the fast transfer of nutrients and pollutants to the top of the food web. We predict that bacterial decomposition will dominate in the hypolimnion of lakes, whereas scavengers will play a determinant role in shallow littoral zones.

Third, we determine the main abiotic variables affecting the decomposition half-lives of carcasses. These include depth, temperature, oxygen levels, and incident light. Oxygen levels and light influence the interactions between carcasses and vertebrate scavengers that, among other cues, use vision to locate food items. Temperature will affect both bacterial and scavenger metabolism. We hypothesize that decomposition half-lives will be shorter in shallow, warm, sunlit, oxygenated areas. On the basis of the available literature on fish decomposition, temperature is the most commonly reported abiotic variable. We propose that temperature can be used as a predictor of decomposition half-lives. We also consider the effect of the flotation of carcasses on the degradation half life.

We further identify the main fish scavengers, during daytime and nighttime, using an underwater custom-made infrared (IR) video system (Chidami et al. 2007), and quantify the contribution of terrestrial scavengers. Our hypothesis is that not all fish species will demonstrate the same interest and level of interaction with carcasses. We also propose that scavengers will display daily and seasonal changes in the intensity of their interactions with carcasses. By revealing the identity of scavengers and their activity patterns, we will be better positioned to determine how matter flows back to the top of the food web during scavenging.

## Material and methods

*Study site*—The study was conducted during summer to autumn 2004 in three boreal lakes located on the Canadian Shield, on the territory of the Station de biologie des Laurentides of the Université de Montréal (Table 1 and Fig. 1). All lakes have a circumneutral pH, are oligotrophic or meso-oligotrophic, and are considered typical of Shield lakes in terms of water chemistry (Carignan et al. 1998, 2000). They are relatively unperturbed lakes and display a gradient in fish species richness. Lake Triton is an unstratified shallow pond, with a small fish community of pumpkinseeds and redbelly dace. Lake Croche is a moderately colored (dissolved organic carbon [DOC]: 5.6 mg L<sup>-1</sup>) stratified lake and sustains a more diverse fish community, dominated by minnows and suckers, than Lake Triton. Lake Cromwell is a shallow, humic (DOC: 8.9 mg L<sup>-1</sup>), stratified lake, with a fish community similar to Lake Croche, but with more catfish (Table 1). These systems were characterized in the field using a YSI1650M probe to measure temperature and oxygen, and with a Licor radiometer to measure light attenuation.

*Burial of falling fish*—We first tested the hypothesis that fish carcasses tend to lie at the surface of sediments, instead of being buried upon deposition. From 10–13 June 2004, 10 carcasses of white sucker were dropped from a boat in the pelagic zones of Lake Croche (five carcasses) and Lake Cromwell (five carcasses). We chose white suckers for this test since they were the most abundant large fish in the studied systems; they were also most likely to be buried upon deposition because of their relative large size. The fish fall was followed and recorded by a remotely operated

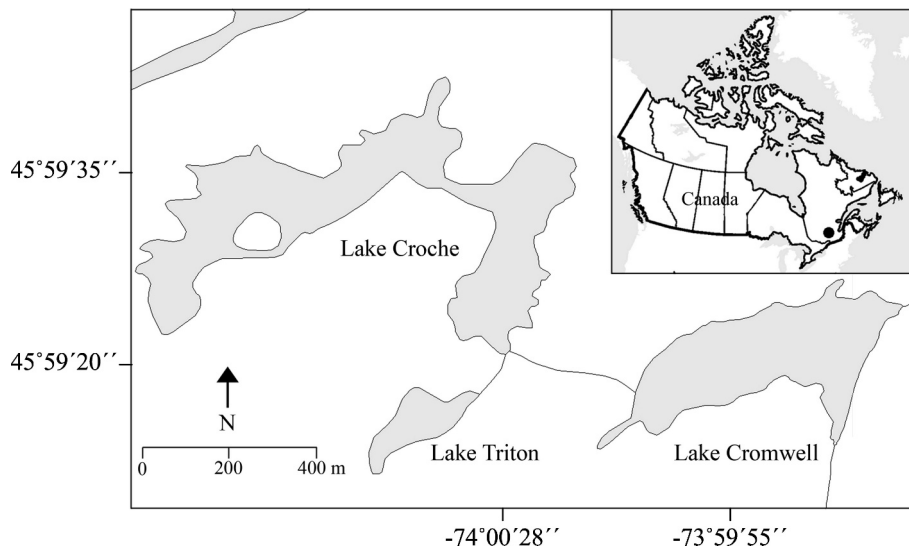


Fig. 1. Maps of lakes Croche, Triton, and Cromwell.

vehicle (VideoRay Scout) equipped with a color video camera, enhanced with two 20-W high-efficiency halogen lights. For easy recovery of the carcasses, the tail was tied to a fishing line. Small phosphorescent flags were attached every 20 cm to the fishing line. Upon deposition, we rated the level of burial of the carcasses on a scale of 0 to 5 (0: no burial; 5: carcass completely buried and no longer visible). Sediment samples were collected from each site of deposition using an Eckman sediment dredge. Sediments were then dried at 40°C during 1 week in an oven, and then weighed. They were placed in an oven at 500°C overnight, and reweighed to determine the organic content. The organic content was determined to help in the interpretation of the results, in the event that different sites had very contrasting sediment characteristics; for instance, a carcass could be more easily buried in sandy sediments with low organic content.

*Modes of decomposition and decomposition half-lives*—To test the hypothesis that vertebrate scavenging is confined to shallow waters and bacterial decomposition prevails at depth, we followed the decomposition sequence of carcasses launched in the three lakes. We further quantified the decomposition half-lives of carcasses in relation to key abiotic variables. Specifically, we assessed the decomposition half-lives of rainbow trout (*Onchorrhynchus mykiss*) ( $342 \pm 42$  g) at different depths in the three lakes, from 04 August to 21 October 2004. Only one fish was placed at each depth of a given transect. Rainbow trout were obtained from a nearby fish hatchery. All fish were killed in a hypoxic water tank during the night before their deposition in lakes.

A series of transects perpendicular to the shoreline were chosen to be representative of the different types of littoral environments found in each lake. Experiments were conducted every meter between 1 and 5 m, and in the deep hole of each system (maximum depth of Lake Cromwell: 9 m; Lake Croche: 11 m; Lake Triton: 4 m). We chose to conduct more intensive experimentation between the

surface and 5 m since it was the region displaying maximal gradients of light, temperature, oxygen, and, presumably, vertebrate activity. At each depth of interest, transects were equipped with a ballasted fishing float (BFF) tied with a solid colorless nylon fishing line. The caudal fin of the carcass was tied with a fishing line to the BFF and allowed only vertical migration of the dead body. At any given time, only one BFF per transect was equipped with a dead trout to avoid a concentration of food, which could change the behavior of scavengers and bias the half-lives.

Carcasses placed between 1 and 5 m were retrieved and weighed daily, until only skin and bones remained. During each retrieval, the position in the water column of the carcass was noted (floating or not), a digital picture was taken, and the integrity of the body was verified. For carcasses placed in the profundal zone (deep hole), carcasses were recovered weekly, because of their long decomposition times.

*Scavenger species*—To identify scavenger species directly interacting with carcasses, we deployed a custom-made underwater video system over a bait (i.e., rainbow trout) during summer 2003 and during fall 2004 in Lake Cromwell at 1 m depth. This video system is fully described in Chidami et al. (2007). Briefly, the underwater video camera and IR projectors were mounted on a stainless steel frame ( $80 \times 80 \times 70$  cm) painted brown to reduce detection by animals. On the shore, videotape recorders were connected to the camera to record fish activity over 24 h. We analyzed the videotapes to identify fish scavengers and to assess the level of their interaction with the bait. We first establish the presence of fish species and number of individuals per species in the field of vision (FOV), using a movie frame (i.e., a still image) taken every 5 min. The cumulative number of fish observed in the FOV over 12 consecutive still images gave the number of individuals on an hourly basis, with units of individual  $h^{-1}$ . We then analyzed all movie frames to quantify the activity of scavengers around the dead fish. The level of activity was

Table 2. Decomposition rates ( $k$ ) and half-lives ( $\tau$ ) for fish carcasses in three boreal lakes.  $n$  is the total number of fish used for the model.

Depth (m)	Cromwell			Croche			Triton		
	$n$	$k$ (d <sup>-1</sup> )	$t_{1/2}$ (h)	$n$	$k$ (d <sup>-1</sup> )	$t_{1/2}$ (h)	$n$	$k$ (d <sup>-1</sup> )	$t_{1/2}$ (h)
1	16	0.0174±0.0041	40	12	0.0102±0.0011	68	4	0.0046±0.0006	151
2	8	0.0078±0.0022	89	8	0.0100±0.0011	69	3	0.0032±0.0011	216
3	3	0.0097±0.0018	72	5	0.0086±0.0014	80	3	0.0042±0.0008	165
4	2	0.0043±0.0008	161	5	0.0068±0.0011	102	3	0.0030±0.0006	231
5	3	0.0009±0.0004	770	3	0.0022±0.0005	315			
9	2	0.0005±0.0001	1,386						
11				3	0.0004±0.000081	1,733			

calculated as the total duration of interaction (seconds of biting or eating) of each scavenger species with the bait on periods of 5 min; the resulting data were then pooled hourly and units of seconds of interactions per hour were used (s h<sup>-1</sup>).

*Statistical analyses*—Fish mass decomposition decreased according to a single-slope exponential decay as observed by others (Minshall et al. 1991; Elliot 1997; Chaloner et al. 2002):

$$\ln(X_t) = \ln(X_0) - kt \quad (1)$$

where  $X_t$  is the remaining mass (g) at time  $t$ ,  $X_0$  the initial mass (g), and  $k$  the constant decay (d<sup>-1</sup>). The mass remaining of all fish carcasses at different days, for each depth and for each lake, was fit with a nonlinear regression model to determinate a mean  $k$ -value and a mean half-life,  $t_{1/2}$  (Table 2).

To compare depth and lake effects, an individual  $k$  constant decay was calculated for each fish carcass deployed. Those  $k$ -values were log<sub>10</sub> transformed to meet assumptions of homogeneity of variance. Log<sub>10</sub>( $k$ -values) were used as the dependent variables and water depth as independent variables. Statistical analyses were carried out using analysis of variance (ANOVA), and post hoc comparisons of depth and lake effects were done with Tukey–Kramer’s studentized range (honestly significant difference [HSD]) tests. Significance levels for all analyses were set at  $\alpha = 0.05$ . Throughout the text, measures of error are presented as standard deviations.

## Results

*Burial of falling fish*—All 10 dropped carcasses stayed at the surface of the sediments upon deposition and showed no sign of immediate burial (the burial index was zero for all carcasses) regardless of depth or nature of sediments (as inferred from percentage organic matter content, which ranged from 44% to 54%). We also followed the burial of carcasses over periods of up to 9 d, but did not witness any signs of burial. The carcasses stayed in the same location. In fact, the postdepositional movement of carcasses was so limited that tissues on the bottom side of the fish clearly underwent a different decomposition process than tissues on the top part.

*Decomposition half-lives and decomposition sequence*—Half-lives were obtained for one fish species (rainbow trout), for three lakes, at different depths and ranged from less than 2 d to more than 2 months (Table 2). Loss of tissue due to decomposition roughly followed an exponential decrease.

In all lakes, half-lives generally varied as a function of depth, temperature, and light penetration (Fig. 2). These relationships were similar between lakes. They were nonlinear; differences in half-lives ( $t_{1/2}$ ) for 0 to 4 m in Lake Croche and Lake Cromwell were not statistically significant, whereas  $t_{1/2}$  at deeper depths were always different from one another (ANOVA with a posteriori HSD;  $p < 0.0001$ ). Note, however, that half-lives in shallow Lake Triton were significantly higher than in the first 4 m of the other two lakes. Half-lives did not systematically increase with oxygen levels, since some short half-lives were recorded at 4 m in the anoxic hypolimnion of Lake Cromwell (Fig. 2B).

We visually followed the decomposition of carcasses using digital photographs taken at each sampling interval (data not shown). Carcasses from the littoral zone were rapidly decomposed and many openings were found within 2–3 d. In contrast, carcasses from the profundal zone were slowly decomposed and no opening was visible during the first few weeks.

*Effect of carcass flotation*—Flotation of carcasses may alter their decomposition rate, and we therefore monitored the frequency and the duration of flotation events for all carcasses (Fig. 3). For all lakes, flotation was only observed for carcasses placed at shallow depths (0 to 4 m), and all flotation events ended with the return of the carcass to the lake bottom within 24 to 48 h. There was a temporal trend in flotation events during decomposition, with 12–23% of all carcasses floating during the first 4 d, 1–11% floating during the next 4 d, and none floating after 8 d (Fig. 3A). Decomposition rates for carcasses having experienced at least one floating event were not significantly different from those of nonfloating carcasses (Tukey–Kramer test on log-normalized data;  $p < 0.05$  for all depths; Fig. 3B).

*Loss of carcasses*—We monitored carcasses daily between 0 and 4 m and noticed that many of them disappeared overnight, even though they were tied to the BFF (Fig. 4). In Lake Cromwell, 50% of corpses at 1 and

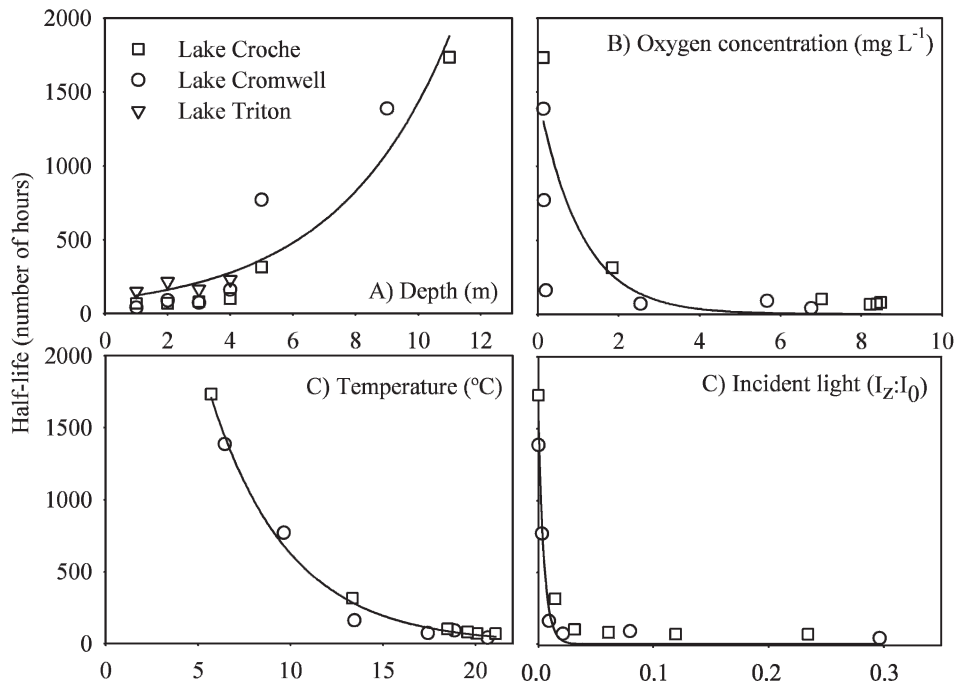


Fig. 2. Relation between decomposition half-lives and (A) depth, (B) oxygen, (C) temperature, and (D) incident light in the three lakes. Exponential relationships on pooled data are described by the following equations: (A):  $t_{1/2} = 93e^{0.27 \times \text{depth}}$ ;  $R^2_{\text{adj}} = 0.92$ ,  $p < 0.0001$ ; (B):  $t_{1/2} = 1,485e^{-0.93 \times \text{oxygen}}$ ;  $R^2_{\text{adj}} = 0.89$ ,  $p = 0.051$ ; (C)  $t_{1/2} = 6,515e^{-0.23 \times \text{temperature}}$ ;  $R^2_{\text{adj}} = 0.99$ ,  $p < 0.0001$ ; (D)  $t_{1/2} = 1,574e^{-202 \times I_z/I_0}$ ;  $R^2_{\text{adj}} = 0.96$ ,  $p = 0.0003$ .

2 m and 33% at 3 m were lost. In Lake Croche, 25% of the dead trout were not retrieved at 1 m and 13% at 2 m. Finally, for Lake Triton 25% of the dead trout were not retrieved at 1 m. All carcasses placed below a depth of 3 m were recovered, suggesting that carcass retrieval is exclusively a littoral process. These losses likely result from the activity of large terrestrial vertebrates. In particular, snapping turtles were seen tearing off dead trout from the BFF. Gulls were also observed eating when carcasses were floating but they were not able to tear off the carcasses from the fishing line.

*Interactions between scavengers and carcasses*—We examined daily and seasonal changes in the presence of scavengers and in the intensity of their interactions (Table 3; modified from Chidami et al. 2007). Overall, only three fish species acted as scavengers: pumpkinseed sunfish (*Lepomis gibbosus*), brown bullhead (*Ictalurus nebulosus*), and creek chub (*Semotilus atromaculatus*).

Seasonal changes in the presence and necrophagous activity of fish were observed (Table 3). For both summer and fall, creek chubs were the most commonly observed and the most active fish species, with an average of around three (fall) and five (summer) individuals present at the same time in the FOV. The mean scavenging activity of creek chubs ranged from 890 s of biting or eating per hour of observation ( $s\ h^{-1}$ ; summer) to  $1,080\ s\ h^{-1}$  (fall). Pumpkinseeds were also present in significant numbers during summertime (1.5 individuals  $h^{-1}$ ), but few interactions were observed with the carcass ( $30\ s\ h^{-1}$ ). During fall, pumpkinseeds were virtually absent and inactive. Brown

bullheads were rarely observed during daytime (average: 0.2 individual  $h^{-1}$  during fall and 0.3 during summer).

Changes in activity of scavengers between night and day were assessed during a fall mission (Table 3). At night, we observed about the same number of creek chubs (1.1 individuals  $h^{-1}$ ) and brown bullhead swimming around the carcass, but the brown bullheads were more actively scavenging ( $1,300\ s\ h^{-1}$ ) than creek chubs ( $290\ s\ h^{-1}$ ). Pumpkinseeds were present in the FOV, but were not directly interacting with the carcass. Nevertheless, they were observed snatching little debris of flesh left by the other scavengers. During daytime, a species switch occurred, with creek chubs being more numerous (2.9 individuals  $h^{-1}$ ) and active ( $1,180\ s\ h^{-1}$ ) than brown bullhead (0.2 individual  $h^{-1}$ ;  $80\ s\ h^{-1}$ ).

## Discussion

*Fish fall and decomposition*—The journey of a dead fish starts with its fall toward the sediments where it can either be buried or stay at the surface, leading to different decomposition outcomes. Our results indicated that in lakes representative of boreal aquatic systems of the Canadian Shield, carcasses were not buried upon impact. They were therefore available for both bacterial degradation and animal scavenging.

We further showed that the ensuing decomposition occurred at a faster rate in shallow, warm, sunlit, oxygenated areas of the lake. Flotation of carcasses was also considered here, but it did not significantly change the observed decomposition rates.

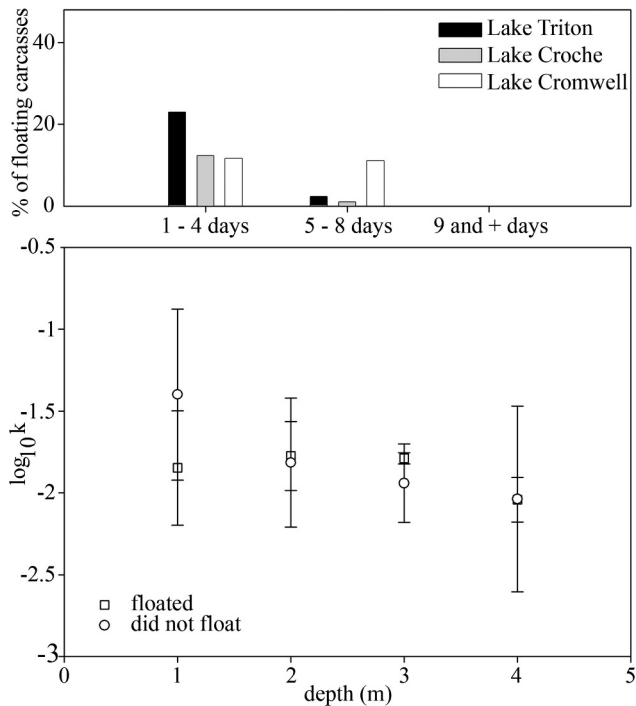


Fig. 3. (A) Histogram representing temporal changes in percentage of total floating carcasses for the first 4 m of depth in three lakes. (B) Mean log-normalized  $k$  values ( $\pm$ SD) as a function of depth for carcasses having experienced at least one floating event (open squares) or having experienced none (open circles). A Tukey–Kramer test revealed no statistical differences between floating and nonfloating carcasses. Data from Lake Croche and Lake Cromwell are pooled since they were not statistically different.

The relationship between decomposition half-lives and abiotic variables was characterized by an exponential decrease. The lack of linearity may indicate that different decomposition pathways were dominating in shallow waters vs. at depth. We propose that vertebrate scavengers were mainly active in the first few meters of the water column, whereas bacterial decomposition predominated at depth. This interpretation is supported by the observation of openings in carcasses (resulting from scavenging activity) only in carcasses retrieved from the littoral zone.

Other studies have reported degradation half-lives for fish carcasses in streams and wetlands. They ranged from ca. 10 to 500 h (Stevenson and Childers 2004; Fenoglio et al. 2005; Chaloner et al. 2002). The only study undertaken in a lake (Schneider 1998) used nonencaged fish, but did not provide a time series for decomposition, and no half-lives can be calculated. The time for complete decomposition of small fish (81–350 mm) was of the order of 18 d for littoral zones (depth  $<2.5$  m) and 27 d for sublittoral zones (depth between 2.5 and 7.5 m). Our data are similar to those obtained by Schneider (1998), although we used larger fish carcasses.

Water temperature was the only environmental data adequately reported in all published studies. When graphically pooling all available data, this variable was found to be correlated to the log-transformed half-lives

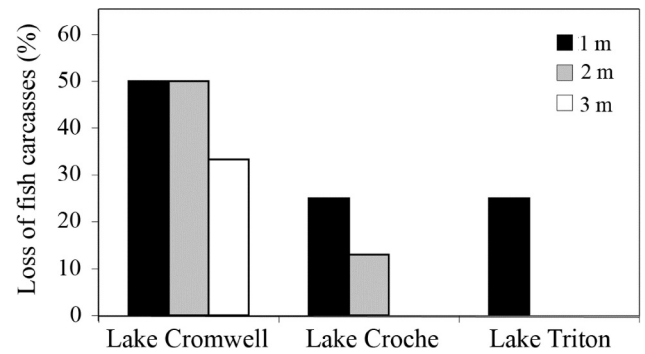


Fig. 4. Percentage of carcass removed from the experiment by large scavengers (e.g., snapping turtles) for the three lakes (Cromwell, Croche, and Triton).

(Fig. 5). For our subset of data, the linear regression on transformed  $t_{1/2}$  was strong ( $R^2_{\text{adj.}} = 0.99$ ,  $p < 0.0001$ ,  $n = 12$ ), and was best described by the following equation:  $\tau = 6515 \times e^{-0.2344 \times T}$ . We suggest that water temperature is a promising surrogate measurement for an approximation of decomposition rates in freshwater systems. However, more studies on other contrasted systems in terms of community composition, depth, and oxygen levels should be conducted to validate the generality of the proposed relationship. This increase in decomposition half-lives with decreasing temperature may be related to lower metabolic activities by decomposing bacteria and scavengers. In lakes, the fact that cold temperatures are found in the profundal zone below the thermocline may also limit scavenger access to the carcass.

Note that, in most studies, carcasses were encaged to prevent scavenging by fish. Since the  $T$  vs.  $t_{1/2}$  relationship holds even when considering encaged carcasses, we suggest that in the absence of fish, an increase in the scavenging activity of macroinvertebrates may sometimes counterbalance the absence of scavenging by fish. Previous studies have already noted that many macroinvertebrate scavengers (e.g., leeches) tend to avoid carcasses surrounded by fish, since they may constitute prey items for fish (e.g., Sarica et al. 2005).

*Interactions between scavengers and carcasses*—We identified creek chubs and brown bullheads as the main fish scavengers in these systems. This indicates that carcasses are used as resources only by a few fish species in our systems. Since Lake Triton is devoid of these species (Table 1), we postulate that the longer half-lives observed in this lake compared with the first 4 m of lakes Cromwell and Croche (Table 2) can be attributed to the lack of fish scavengers. In this particular case, the absence of vertebrate scavengers is not counterbalanced by the presence of an efficient community of invertebrate scavengers.

Note that creek chubs and brown bullheads are mainly omnivorous (Scott and Crossman 1974). They have been shown to feed on zooplankton and zoobenthos, but not on fish carcasses. However, studies of gut contents can easily overlook boneless fish fragments resulting from scavenging activities. The daily scavenging activity patterns reported here (with brown bullheads being very active at night) are

Table 3. Summary of daily interactions between scavengers and carcasses recorded with an underwater IR video system at 1 m in Lake Cromwell during summer 2003 and fall 2004. Mean scavenger frequencies ( $\pm$ SD) and levels of activity are presented for two seasons during the day and for day vs. night during the fall. The density was measured every 5 min and averaged over 1 h. nq, not quantified.

Scavengers	Time of day	Fish frequency (individuals h <sup>-1</sup> )		Scavenging activity (s h <sup>-1</sup> )	
		Summer	Fall	Summer	Fall
Brown bullhead	Day	0.3 $\pm$ 0.6	0.2 $\pm$ 0.7	453 $\pm$ 685	91 $\pm$ 154
	Night	nq	1.1 $\pm$ 1.0	nq	1,305 $\pm$ 597
Creek chub	Day	4.6 $\pm$ 4.1	2.8 $\pm$ 2.6	899 $\pm$ 653	1,078 $\pm$ 492
	Night	nq	1.2 $\pm$ 1.7	nq	300 $\pm$ 335
Pumpkinseed	Day	1.5 $\pm$ 1.4	0.0 $\pm$ 0.2	46 $\pm$ 57	0 $\pm$ 1
	Night	nq	0.0 $\pm$ 0.0	nq	0 $\pm$ 0

consistent with known patterns of general activity for these species (Scott and Crossmann 1974).

**Biogeochemical implications**—Overall, this study indicates that fish decomposition is relatively rapid in shallow waters ( $t_{1/2}$  between ca. 2 and 10 d), and is driven partly by interactions with some fish species. This fast recycling of fish tissues may explain the scarcity of direct observation of fish carcasses in the littoral zone of lakes. It may also affect pools and fluxes of nutrients and contaminants.

In the following, we will demonstrate the role of carcasses in nutrient cycling by using Lake Croche as an example since this lake has been the site of many limnological studies and many data sets are available. It is also quite representative of oligotrophic Canadian Shield lakes in terms of morphometry and water chemistry (Carignan et al. 2000). We will focus on one nutrient, phosphorus, since it is the main limiting factor in Canadian Shield lakes (Lafond et al. 1990). We will consider one source of fish carcass, namely the white sucker population, since it is the largest in the lake in terms of biomass, and the best described in terms of mortality and population dynamics. Indeed, Verdon (1976) reports fish growth, annual mortality, and annual fish biomass for each age class of white sucker in two basins of Lake Croche. We here

assume that white suckers of 2 yr and older cannot be eaten by the piscivorous brook trout and lake trout present in the lake, since they reach a size of about 12 to 14 cm within 2 yr. From Verdon's annual mortality rates and fish biomass, we estimate an approximative carcass biomass of 502 kg yr<sup>-1</sup> for the east basin of Lake Croche. Assuming a P content in fish tissue of 0.5% (Lewin et al. 2003), carcass biomass from white suckers is 2.5 kg of P, representing 68% of the aqueous P pool (i.e., 3.7 kg of P in a water column with a total P [TP] of 10  $\mu$ g L<sup>-1</sup> and a volume of 366,196 m<sup>3</sup>; Lafond et al. 1990; Carignan et al. 2000). Note that we here consider only dissolved and particulate P in the aqueous P pool, not P bound to large planktonic organisms and fish. For comparison, we also calculated the pool of TP in fish and water for a similar Canadian Shield lake (Mouse Lake; Demers et al. 2001; Hudson et al. 2001) and found a similar ratio of 65%. If we assume that P sedimentation rates in Lake Croche are similar to other Canadian Shield lakes of similar size and water chemistry (i.e., 0.8 mg m<sup>-2</sup> d<sup>-1</sup> P; Hudson and Taylor 2005), we can estimate that, on an annual basis, water-to-sediment fall of white sucker carcasses alone corresponds to about 13.5% of the particulate P sedimentation rate in the east basin of Lake Croche (Fig. 6). Note that the quality of carcass-bound P in terms of food attractiveness likely differs from particulate P. Also, a significant fraction of P in fish is found in bones and scales (Kitchell et al. 1975) that may be less bioavailable than organic particulate matter. Other studies have mentioned that fish fall could be an important flux of P in lakes. For instance, Kitchell et al. (1975) calculated that in late spring and early summer, bluegill mortality could lead to influx of mineralized P at levels higher than allochthonous inputs in a Wisconsin lake. Further, Nriagu (1983) demonstrated that fish debris could represent up to 20% of the vertical flux of P to the littoral sediments of Lake Erie. Finally, Nakashima and Leggett (1980) assessed that nutrient release due to fish decomposition supplied up to 20% of the allochthonous P entering the south basin of Lake Memphremagog in the spring.

According to the results presented here, the fate of this significant flux of sucker-bound P will be different whether the carcass is deposited in the littoral vs. the pelagic zone (Fig. 6). A fish dying in the pelagic zone during the summer will be deposited at the surface of the profundal sediment under the thermocline where it will be slowly degraded by

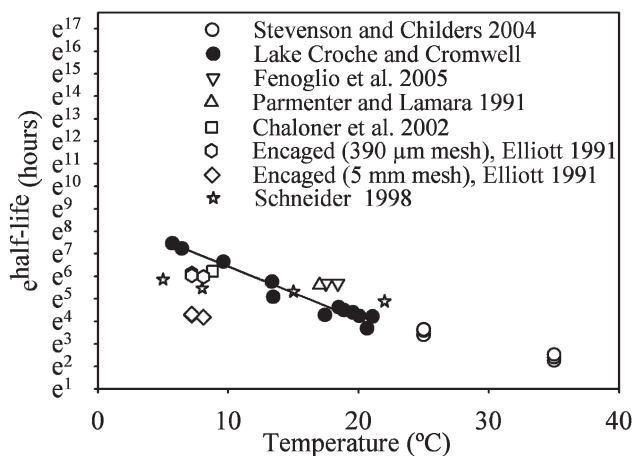


Fig. 5. Relation between half-lives found in the literature, data from the Lake Croche and Lake Cromwell, and the temperature. A nonlinear regression was performed only for our data ( $R^2 = 0.99$ ;  $p < 0.0001$ ).

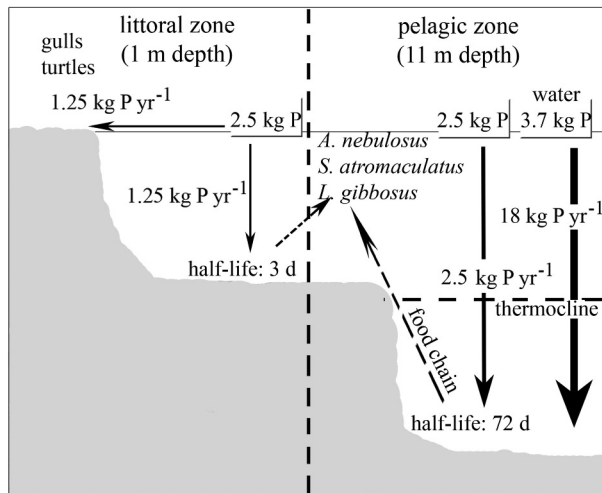


Fig. 6. Schematic representation of the effect of carcass falls on the phosphorus cycle in the littoral vs. the pelagic zone of Lake Croche. Solid arrows represent P fluxes and their width is proportional to the importance of the flux. Dashed arrows represent decomposition half lives.

bacterial processes over months. The mineralized P will not be available for biomass growth before fall turnover, and it will re-enter the food chain through primary producers. The transport of this P back to the fish biomass will be further delayed by the presence of at least two trophic transfer steps. In sharp contrast, a fish dying in the littoral zone will be degraded in a matter of days mostly by terrestrial and aquatic vertebrates (in approximately even proportion between each group; Fig. 6). Therefore, carcass-bound P will be directly and rapidly reincorporated near the top of the aquatic and terrestrial food chains during the same growing season.

In the case of contaminants that tend to biomagnify along food chains, this contrast between the fate of carcasses in littoral and profundal zones will have an additional consequence. Vertebrate scavengers from littoral zones will feed near the top of the trophic web and hence, will be exposed to the most contaminated aquatic prey items available in the system, and biomagnify the contaminants once more. In contrast, in the profundal zones, contaminants will be returned to the base of the food chain and start a new biomagnification cycle that may take months to years to complete, depending on the contaminant (Harris et al. 2007). It is therefore likely that lakes with very few vertebrate scavengers will more rapidly respond to decreases in contaminant inputs than lakes with large scavenger communities.

In a more general limnological context, the role of fish on nutrient cycling in the absence of a massive mortality event is considered to be mainly through excretory processes, translocation of large living individuals, effects on prey, and modification of the physical environment (Vanni 2002). We here argue that natural fish fall may in some cases constitute a significant flux. We further hypothesize that this effect will be more important in lakes with significant populations of benthivorous or planktivorous (or both) fish submitted to no or low fish predation.

Much uncertainty still remains with respect to natural mortality rates of fish, and consequently, future research is needed to provide estimates of carcass biomass in lakes. But, as shown here, these estimates will have to take into account the location of the carcasses in the lake to link them to biogeochemical fluxes.

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