

Response to “Comparative estimate of P fluxes in lakes” by J. M. Sereda and J. J. Hudson

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Sereda and Hudson (2010) are commenting on a carcass-bound phosphorus (P) flux estimate reported in an article by Chidami and Amyot (2008). This article mainly presents in situ experimental evidence on the factors affecting fish degradation in lakes. To place these field results in a biogeochemical context, Chidami and Amyot (2008) concluded their paper by presenting an estimate of some selected phosphorus fluxes in one of the studied lakes. For P fluxes related to carcass fall, we used estimates of white sucker (*Catostomus commersoni*) mortality rates from Verdon (1976) because it was the only full data set available on fish population dynamics in one of the studied lakes. In their comment, Sereda and Hudson (2010) consider that the fish mortality rates are anomalous, that the reported P fluxes due to carcass fall are too high, that other fluxes should have been considered, and that bone decomposition was not monitored. In the following, we will address each of these points.

Fish mortality rates—One of the main points of Sereda and Hudson (2010) is that the fish mortality rates used in calculating the carcass-bound P flux were anomalous. The details of our calculation of carcass biomass for the East basin of Lake Croche are given in Table 1. The mortality rates reported by Verdon (1976) were consistent with those from other studies done on the same fish species in the area (Fortin 1967). Contrary to what Sereda and Hudson (2010) indicate, the annual mortality rate that we used was not of 88%, but rather ranged from 21% to 90%, depending on the age class (Table 1). Also, Sereda and Hudson (2010) indicate a total white sucker biomass of 681 kg for the whole lake, citing Verdon and Magnin (1977), when in fact these authors reported a total white sucker biomass of 956 kg, for the East basin alone in 1973. Verdon (1976) calculated mortality rates by estimating the loss of individuals per age class from 1973 to 1974; therefore, 1973 is the reference year for the mortality rates. The sample size and methodology for assessment of mortality rates were adequate (i.e., overall, 2588 individuals were used in Verdon’s study, for a population of around 4300). So, our estimates on carcass biomass are valid.

Even though we maintain that our mortality rates are valid, they might still be higher than average for lakes of similar size and productivity, as stated by Sereda and Hudson (2010), due to two factors. Our estimates were done for the East basin of Lake Croche, where white suckers were historically known to congregate (Verdon 1976), therefore locally increasing fish

densities and also our estimates of carcass fall. A carcass-bound P flux estimate combining the two basins would yield a smaller value. Also, Verdon’s study is more than 30 yr old and provides only 2 yr of data; it is likely that fish dynamics have changed over time and that a longer and more recent temporal monitoring would yield better estimates of fish carcasses. In particular, we believe that one of the historical spawning grounds for white suckers in Lake Croche has been disturbed by human activities, with possible, but unknown, adverse consequences for the white sucker population.

Importance of fish carcass fall in other Canadian Shield lakes—To further consider Sereda and Hudson’s comment on the importance of carcass-bound P flux in oligo–mesotrophic Canadian Shield lakes, we examined the literature for other complete data sets on fish population dynamics from which estimates of fish mortality not due to predation could be derived. We chose a large and complete data set from Mouse and Ranger lakes, two southeastern Ontario lakes that were used by Sereda and Hudson to calculate their fluxes (Hudson and Taylor 2005; Sereda et al. 2008). These lakes were studied intensively from 1991 to 1997. In August 1993, a biomanipulation was undertaken during which a large number of predators from Ranger Lake were transfer to Mouse Lake (Demers et al. 2001a). Here, we focus on the premanipulation years of the study. At that time, Mouse Lake harbored seven fish species, none of which was piscivorous, whereas Ranger Lake had 10 fish species, including two piscivores: largemouth bass (*Micropterus salmoides*) and smallmouth bass (*Micropterus dolomieu*). We used fish bioenergetics models to estimate production and consumption for both piscivores and nonpiscivores. The full data set and details on parameter estimation are given in Demers et al. (2001b). Briefly, our bioenergetics model was based on rates of growth for all year classes (age 0 to oldest for each species) of all the major fish populations during each of the 3 yr in both lakes. The models were also based on observed epilimnetic water temperatures and species-specific and year class-specific estimates of diet composition on the basis of stomach content analyses. We first calculated the total biomass of fish dying during each year t (BD_t ; deaths from predation and all other causes) for each species and each year class. This was done with the use of Eq. 1,

$$BD_t = B_t + P_t - B_{t+1} \quad (1)$$

where B_t is the living biomass at the beginning of year t , P_t is the yearly production (calculated as the sum of daily production over the year), and B_{t+1} is the living biomass at the end of year t .

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Table 1. Number of fish, annual mortality rates, and yearly carcass biomass estimates of white suckers in the East basin of Lake Croche with data from Verdon (1976).

Age	Number of fish in 1973	Annual mortality rate	Number of carcass	Average weight of carcass (g)	Total mass (kg)
2	1369	0.21	289	22	6
3	387	0.27	103	81	8
4	1937	0.27	515	139	72
5	1146	0.41	464	195	91
6	955	0.76	728	256	187
7	573	0.90	516	272	140
Total mass					504

Yearly biomass of fish dying from causes other than predation (BNP_t) was then assessed with the equation

$$BNP_t = BT_t - BP_t \quad (2)$$

where BP_t is the biomass of fish dying from predation in year t , reported in Demers et al. (2001*b*). Note that for year class 0+, we did not have estimates of initial population sizes (i.e., estimates of larval densities). For this year class, we therefore applied a mortality rate taken from the literature (Roell and Orth 1993; Lorenzen 1996).

Using 1993 as a reference year, we calculated a total biomass of fish carcasses of 1000 kg km^{-2} for the lake with piscivores (Ranger Lake) and 3800 kg km^{-2} for the lake without piscivores (Mouse Lake). In terms of downward P fluxes induced by fish fall, it translates into fluxes of $5.1\text{--}19 \text{ kg P km}^{-2}$ for Ranger Lake and Mouse Lake, respectively. According to Hudson and Taylor (2005), sedimentation fluxes of P for the same year (1993) in the same lakes were 350 and 330 kg P km^{-2} for Ranger Lake and Mouse Lake, respectively, so fish fall represented 1.5% (Ranger) to 5.8% (Mouse) of the sedimentation flux of P. In Chidami and Amyot (2008), we obtained a higher value of 13.5% . We conclude that the importance of fish fall as a downward flux of P in these two oligo-mesotrophic Canadian Shield lakes is relatively small and roughly in agreement with the calculations of Sereda and Hudson (2010). The importance of this flux might differ markedly from one lake to the other. In lakes with no piscivores, it is anticipated that carcass flux will be more significant, whereas in lakes where predation pressures are important, fewer carcasses will fall and the associated P flux will be often insignificant.

On the importance of other P fluxes in lakes—In our illustrative calculation of phosphorus, we elected to compare the carcass-bound P flux to the other main epilimnion-to-sediment P flux (i.e., sedimentation of particulate matter). Sereda and Hudson (2010) do not dispute this calculation but argue that other fluxes should have been included to give a more complete picture. We agree with Sereda and Hudson (2010) that P regenerated by fish excretion and planktonic regeneration are major fluxes in oligo-mesotrophic lakes and that sedimentation of feces from fish could be a significant contributor to total P sedimentation. We agree that these P fluxes are often significantly higher than fluxes induced by carcass fall. However, it is important to stress that the fate of P associated with these various fluxes will

differ from P bound to carcasses, particularly in shallow waters. In this latter case, scavenging by invertebrates, fish, and other vertebrates will lead to P recycling at a higher level of the food web, compared with other processes. Sereda and Hudson (2010) refer to this process as the vertebrate loop. In contrast, P regeneration by fish and zooplankton will mainly sustain primary production in the water column. As mentioned in Chidami and Amyot (2008) and recognized in Sereda and Hudson (2010), the so-called “vertebrate loop” might have important biogeochemical implications, particularly for other compounds such as biomagnifiable contaminants.

Degradation of bones and scales—We also mentioned, as did Sereda and Hudson (2010), that a significant fraction of P in fish is found in bones and scales (Kitchell et al. 1975). P associated with bones and scales will be recycled at a slower rate than P associated with soft tissues. The half-lives reported in Chidami and Amyot (2008) are therefore applicable to soft tissues, not bones and scales. It is of note that Nriagu (1983) concluded that fish bones are rapidly remineralized through redox-independent biological processes in sediments of Lake Erie; $10\text{--}50\%$ were degraded in 3 weeks. He estimated that fish debris could account for well over $10\text{--}20\%$ of the P flux to the sediments. More studies on the biomineralization of fish debris in Canadian Shield lakes are needed.

In summary, we conclude that carcass fall represents about $1\text{--}6\%$ of downward P fluxes in some oligo-mesotrophic lakes, with higher estimates in lakes without piscivores. This flux might represent more than 10% of downward fluxes in areas of a lake where fish tend to congregate. Carcass fall represents a small flux compared with P regeneration by fish and invertebrates but affects different parts of the ecosystem. To better assess food web effects of carcasses, a fuller study in which key fluxes could be measured simultaneously and subsequently modeled would be warranted. Such a study should evaluate nonpredatory fish mortality for different species living in different fish communities and should follow the movement of nutrients, contaminants, or both from carcasses to food webs. Transplantation of isotope-labeled carcasses in pristine lakes could allow the tracking of elements originating from carcasses through the food web, as demonstrated by Sarica et al. (2005). One major hurdle for such a study is the variety of scavenger communities found in boreal lakes. For instance, we previously

described scavenger communities dominated by invertebrates, with leeches sometimes being key scavengers (Sarica et al. 2005), whereas in Chidami and Amyot (2008), fish, terrestrial vertebrates, and bacteria seemed mostly responsible for carcass degradation. Ultimately, the composition of the scavenger community and the density of the main scavenger species could determine the food web fluxes most influenced by carcasses.

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