

Comparative estimate of P fluxes in lakes: A comment on “Fish decomposition in boreal lakes and biogeochemical implications” by Chidami and Amyot (2008)

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The contribution of fish and their relative importance in the nutrient dynamics of lakes (sink vs. source) continue to be a topic of debate (Mehner et al. 2007; Wurtsbaugh 2007; Sereda et al. 2008b). Much of this debate is a result of the context under which fish are compared (Hudson et al. 1999; Wilhelm et al. 1999). Fish represent an internal regenerative pathway of nutrients and in turn should be compared with other internal pathways (i.e., internal loading from the sediments and planktonic regeneration). However, studies continue to conclude that the regeneration or recycling of nutrients from fish (through excretion or decomposition) are a significant source of phosphorus (P) by comparing fish with a single and often trivial supply route such as allochthonous inputs (Kitchell et al. 1975; Schaus et al. 1997; Schindler et al. 2001).

A recent study by Chidami and Amyot (2008) offered novel insight into the role of fish in the phosphorus cycle of lakes. The authors sought to test several key hypotheses concerning the fate of fish carcasses in limnetic systems. Most notably, Chidami and Amyot (2008) ask whether fish carcasses are buried upon deposition, and if not, what is the half-life of the carcass undergoing vertebrate scavenging or bacterial decomposition. The authors concluded that fish were not buried upon deposition and thus were susceptible to both vertebrate scavenging (littoral zone) and bacterial degradation (hypolimnion). Chidami and Amyot (2008) point out that water temperature may be used to estimate rates of fish carcass decomposition. The empirical relationships they provide add to a growing literature of empirical models that provide the ability to calculate rapidly rates of internal nutrient recycling (Nurnberg 1984; Hudson and Taylor 2005; Sereda et al. 2008a). They calculated that carcass biomass of a single species (white sucker, *Catostomus commersoni*) could account for 68% of the aqueous P pool, and natural mortality of this species was equivalent to 13.5% of particulate P sedimentation in Lake Croche. The authors concluded that fish carcasses might represent a significant flux of P. This latter point is where we disagree with authors Chidami and Amyot.

Chidami and Amyot (2008) have calculated that a natural mortality (502 kg of biomass) of a single species (white sucker) could account for an annual flux of 2.5 kg P in the East basin of Lake Croche. However, we suspect that these values are anomalous and do not reflect the contribution of natural fish mortalities to nutrient fluxes in oligo-mesotrophic lakes. Chidami and Amyot (2008) have based these calculations on estimates of white sucker biomass and mortality, which have been reported in a study

by Verdon and Magnin (1977). Verdon and Magnin (1977) estimated a standing stock of white sucker biomass of 2900 kg km⁻² (681 kg total lake-wide biomass), with ~84% of the white sucker population (~ 572 kg) residing in the East basin of Lake Croche. Therefore, the standing stock of white suckers in the East basin (0.06 km²) is 9500 kg km⁻², a biomass considerably greater than what has been reported for other oligo-mesotrophic Canadian shield lakes (for the entire fish assemblage, mean = 3000 ± 700 SE kg km⁻², n = 26; Fraser 1981; Kelso 1985; Kelso and Johnson 1991). Furthermore, Chidami and Amyot (2008) estimate that 88% (502 kg; 74% of the lake-wide standing stock) of the white sucker biomass in the East basin is lost annually to natural mortality. If we account for annual production of white suckers, 163.8 kg (~ 138 kg for the East basin) (Verdon and Magnin 1977), an annual mortality of 502 kg would still represent 71% of the white sucker biomass. These estimates are greater than estimates of annual fish mortality reported by other studies: a range of 10–67% (Lorenzen 1996; Schneider 1998; Mills et al. 2002) with a mean of 25% (Reznick et al. 2002). Consequently the large flux of P from white sucker carcasses in the East basin of Lake Croche is a result of an exceptionally great density of fish biomass and abnormally high annual mortality rate. On the basis of mean standing stock estimates for oligo-mesotrophic Canadian shield lakes (3000 kg km⁻²), typical mean total fish biomass (all species combined) would be approximately 180 kg for the East basin (or ~ 570 kg for the entire lake, 0.19 km⁻²). Assuming a range in annual mortality rate of 10–67% (Lorenzen 1996; Schneider 1998; Mills et al. 2002), we estimate carcass biomass from annual fish mortality to be approximately 18–121 kg, or 4–24% of the author's estimate for only white suckers. In turn, fish carcasses might only represent a P flux of 0.09–0.61 kg instead of 2.5 kg.

However, regardless of the estimate of fish biomass or the rate of mortality applied, we contest the notion that fish carcasses (in the absence of mass mortality events) represent a significant flux of nutrients in lakes. For comparison, we have applied the equations of Sereda et al. (2008a) to conservatively calculate the mass of P regenerated through excretion by an equal mass (502 kg) of fish. Excretion rates were calculated for only the summer months (June through September) when water temperatures are highest and the contribution of fish excretion to the nutrient supply is expected to be most significant. Furthermore, we calculated rates of planktonic P regeneration for epilimnetic waters in the East basin during the summer months (June through September) by applying the

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equation of Hudson and Taylor (2005) to a mean total phosphorus (TP) of $10 \mu\text{g L}^{-1}$ (Chidami and Amyot 2008). Epilimnetic volume was assumed to account for 67% of lake volume (based on mean lake depth = 5.1 m and a mean summer mixing depth of 3.4 m; Carignan et al. 2000). Total lake volume was $877,000 \text{ m}^3$ (Chidami and Amyot 2008), and the East basin accounted for approximately 30% of the total lake area. Approximately $4.0 [\pm 0.49, 95\% \text{ confidence interval (CI)}]$ kg and $25 (\pm 0.04, 95\% \text{ CI})$ kg P could be regenerated by fish and plankton, respectively. Thus, the P supplied (2.5 kg) by the annual mortality of white suckers is approximately 63% and 10% of the P regenerated by fish excretion and plankton, respectively. However, on the basis of our estimates of fish biomass (180 kg), the P supplied from fish carcasses (18–121 kg) only represents 7–48% and 0.4–2% of the P regenerated by fish excretion and planktonic regeneration, respectively.

Chidami and Amyot (2008) estimated that the downward flux of P (2.5 kg) in fish carcasses may be equivalent to 13.5% of particulate P sedimentation. However, on the basis of our biomass estimates, the downward flux of P (0.09–0.61 kg) in fish biomass may only equal 0.5–3% of particulate P sedimentation in oligo–mesotrophic lakes. Furthermore, our estimates of P excretion by fish are conservative and do not account for nutrients egested as feces. Approximately 50% of all nutrients released by fish may be egested as feces, which can then be deposited in the sediments (Porter et al. 1987; André et al. 2003). Therefore, by comparison, the downward flux of egested nutrients (i.e., feces) by fish may be 47–93% greater than rates of nutrient deposition through the loss of fish carcasses.

Furthermore, Chidami and Amyot (2008) did not monitor all of the decomposition of the fish (i.e., bones and scales) when calculating decomposition half-life. Approximately 50% of fish P could be sequestered in recalcitrant bone and scale (Kitchell et al. 1975; Parmenter and Lamarra 1991). Therefore, the half-life calculated by the authors could represent the decomposition and presumably release of only 50% of all of the P bound in fish carcasses. Moreover, up to 50% of the fish carcasses deposited in the littoral zone might be scavenged and removed from the system by terrestrial vertebrates (Chidami and Amyot 2008). Therefore, of the 2.5 kg of TP in fish carcasses (assuming 100% deposition in the littoral zone), 1.25 kg TP might be removed from the system by terrestrial vertebrates (Chidami and Amyot 2008, fig. 6). Of the remaining 1.25 kg TP, only half of the TP (0.625 kg) not in bone and scales may be susceptible to rapid degradation. Thus, the annual mortality of white suckers may contribute only 16% and 2.5% (or 2–12% and 0.09–0.61% on the basis of our fish biomass estimates) of the P supplied through fish excretion and planktonic regeneration, respectively. These inputs might be even less if there are further losses of P to direct sediment binding while the carcasses decompose on the sediments.

Finally, in the presence of scavenging fish species, TP sequestered in fish carcasses might be directly returned to the top of the food chain through a “vertebrate loop” (Chidami and Amyot 2008, fig. 6). Despite rapid decom-

position rates, the recycling of P within a vertebrate loop re-enforces the role of fish as a nutrient sink rather than a source for primary producers in lakes. Considering fish carcasses are rarely observed in shallow lakes, the transfer of fish-derived nutrients into terrestrial and aquatic vertebrates might be a dominant pathway (Schneider 1998).

In summary, we believe that Chidami and Amyot (2008) have overstated the importance of fish carcasses to the P flux of lakes. The large flux of P (2.5 kg) reported by Chidami and Amyot (2008) results from an exceptionally great density of fish biomass (9500 kg km^{-2}) and an abnormally high annual mortality rate (88%). Consequently, the contribution of fish carcasses to the P flux in Lake Croche is not indicative of most oligo–mesotrophic lakes. The significance of fish carcasses to the nutrient flux in lakes is minor when compared with other internal pathways (e.g., excretion and egestion by fish and planktonic regeneration). However, fish might function as a significant nutrient sink by sequestering nutrients that can be returned to the top of the food chain through a vertebrate loop or lost from the system through scavenging by terrestrial vertebrates (Chidami and Amyot 2008). Further research on the fate of fish bones and their significance on the long-term sequestering of P in lakes is required. Despite our focus on P fluxes, we assert that similar conclusions would be attained for other nutrients and possibly contaminants.

Nonetheless, we commend Chidami and Amyot (2008) for applying a novel approach to determining the fate of fish carcasses in lakes. The authors have demonstrated that fish carcasses might not be buried upon deposition and are susceptible to bacterial and vertebrate scavenging. Furthermore, the authors demonstrate that water temperature might be a promising predictor of fish decomposition rate. Their empirical models could be applied to aquatic ecosystems in which estimates of fish mortality are available. A comprehensive understanding of internal P recycling is developing, and the relevance of any single regenerative pathway to the overall nutrient budget of a lake might soon be determined.

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