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The role of insectivorous fish in fostering the allochthonous subsidy of lakes

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Recently, Wurtsbaugh (2007) commented on our earlier report in which we quantified the nutrient subsidy by a facultative insectivorous fish (bleak, *Alburnus alburnus*)

feeding on terrestrial insects in a 0.12 km² lake (Großer Vätersee, Germany) (Mehner et al. 2005). We showed that the annual consumption rate of bleak consisted of about 84% terrestrial insects. We estimated that the allochthonous phosphorus included in these insects represented about 2.1% of the lake's internal total phosphorus (TP) concentration, whereas excretion of P by fish was equivalent to about 11% of the mean epilimnetic soluble reactive phosphorus (SRP) concentration. Accordingly, we concluded that the lake studied was only weakly subsidized by allochthonous phosphorus stored in insects. Based on a decay model with varying parameters that calculated the spatial distribution of the daily fallout of terrestrial insects into lakes, we concluded that the subsidy by terrestrial insects to fish consumption and lake nutrient pools was likely most important in small, oligotrophic lakes surrounded by forests.

Wurtsbaugh identified three possible shortcomings in our analyses. First, he argues that insects consumed by fish

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have already fallen into the lake, so they are already part of the internal lake nutrient budget. Second, he argues that the comparison of an annual nutrient processing rate with an in-lake concentration is problematic. He suggests, instead, comparing the daily P-excretion rate of fish with the total phosphorus concentration. Third, Wurtsbaugh questions whether our decay model correctly mirrors the fallout of terrestrial insects to lakes. Here, we respond to all arguments in the same sequence.

First, we fully agree with Wurtsbaugh that lakes receive nutrients from their surroundings mainly passively. The majority of terrestrial insects that are trapped at the surface become part of the nutrient budget of the lake immediately after their death. Thus, fish are not irreplaceable agents in making allochthonous nutrients available to the lake, and in the long-term perspective, lakes are sinks for external nutrients bound in insects even if they do not harbor insectivorous fishes. This argument is true, but the reason why we estimated the rates by which fish process nutrients was to understand the mechanisms contributing to the allochthonous subsidy of lakes. Due to the large magnitude in size between aquatic organisms and the exponential scaling of metabolic laws with body size, we would expect nutrient processing by bacteria, phytoplankton, zooplankton, and fish to occur at strongly differing spatial and temporal scales. We will discuss these issues again below.

Wurtsbaugh's second argument is that we compared the annual rates of nutrient processing by fish with a nutrient concentration or a pool by assuming static conditions. In fact, however, nutrient pools are repeatedly recycled in the lake during each growing season. This objection by Wurtsbaugh is legitimate, and we have to admit that we did not consider the different time scales of the processes properly. Wurtsbaugh suggests comparing the daily excretion rate of bleak with the TP concentration. However, the focus on daily rates and lakewide TP pools is, in a way, similarly arbitrary. Pelagic nutrient turnover rates have seldom been quantified. Lean (1973) described an almost complete uptake of radioactive phosphate by lake water, which included algae, bacteria, and nonliving particulate matter, in less than one hour. From our perspective, this estimate is not identical with Wurtsbaugh's (2007) conclusion (based on the same paper) that TP cycles within minutes to hours. A comprehensive overview is given by Hudson et al. (1999), who estimated that the turnover rate of total particulate phosphorus in 20 lakes was almost constant at 0.2 d^{-1} , with no relationship to TP concentration in the lakes. Hence, TP would be recycled within about five days. During this period, however, a portion of particulate P is lost by sinking out of the epilimnetic layers and hence is no longer directly available for phytoplankton production, at least as long the lake remains stratified (Güde and Gries 1998; Kleeberg 2002). Accordingly, Wurtsbaugh's suggestion to compare daily fish excretion rates with the lakewide TP pool leads to erroneous results.

To shed light on the question of how strongly Lake Großer Vätersee is subsidized by allochthonous phosphorus, the insect-derived P flux from fish to the lake has to be compared with the P flux from diffuse sources that enters the lake annually. Unfortunately, data on diffuse P loading

are not available. As a proxy, we have estimated the theoretical P loading from the annual mean TP concentration in the lake using Vollenweider's (1976) empirical equation. The lake has no surface inflow or outflow, and its exchange rate with groundwater is low (Wille 2002). Using the hydrological data provided by Wille (2002), the water residence time was calculated at about nine years. Based on an average in-lake TP concentration of 32.6 mg m^{-3} (Mehner et al. 2005), the diffuse external P load would be predicted to not exceed $0.075 \text{ g m}^{-2} \text{ yr}^{-1}$ (total lakewide rate $9,088 \text{ g yr}^{-1}$). The terrestrial-derived phosphorus consumed annually by bleak (431.6 g yr^{-1}) is hence equivalent to about 4.7% of the diffuse P load to the lake. This estimate is close to our earlier prediction. Additionally, the estimates of the annual amount of allochthonous P excreted by bleak (210.6 g P within 180 d or $1.86 \text{ } \mu\text{g P m}^{-3} \text{ d}^{-1}$; Mehner et al. 2005) can be compared with the P demand of primary production in Großer Vätersee. The average primary production of phytoplankton was $388 \text{ mg C m}^{-2} \text{ d}^{-1}$ between May and October 2002 (P. Kasprzak unpubl. results, Leibniz-Institute of Freshwater Ecology and Inland Fisheries), which converts into $73.5 \text{ mg C m}^{-3} \text{ d}^{-1}$ if the entire lake volume is considered. By using the Redfield ratio (atomic C:P = 106:1 or mass ratio C:P = 40:1; Redfield 1934), this production rate converts into a P demand of $1.85 \text{ mg P m}^{-3} \text{ d}^{-1}$. Accordingly, the daily excretion rate by bleak of allochthonous P covered 0.10% of daily P demand of the primary production. Both calculations given here correctly compared rates, and they point to the fact that the contribution of fish feeding on terrestrial insects to internal lake P pools is probably relatively low. Here we agree with Wurtsbaugh (2007), who estimated a similarly low contribution of bleak to P recycling ($0.006\% \text{ d}^{-1}$ or $2.2\% \text{ yr}^{-1}$). However, the overall importance of P subsidy by bleak is underestimated if it is directly compared with other P sources from the terrestrial watershed. Bleak transform the phosphorus and supply it directly to phytoplankton, since fish excrete P in bioavailable form (Brabrand et al. 1990). In addition, the supply is spatially coupled with the phytoplankton occurrence, since bleak never migrate below the thermocline (J. Ihlau unpubl. results), such that all excreted P remains in the epilimnetic layer.

Third, Wurtsbaugh (2007) questions our approach to estimating the insect fallout to lakes by a decay model. He refers mainly to two earlier papers by Norlin (1964, 1967) and asserts that Norlin suggested that most terrestrial insects enter lakes via drift of "aerial plankton" over large distances and are deposited evenly over the lake surface. Accordingly, small and large lakes would receive similar areal deposition rates, in opposition to our conclusion that small lakes receive higher fallouts since insects are derived from the shoreline vegetation. However, Norlin explicitly stated that "most of the drifting fauna on the surface of the lakes is probably derived from the surrounding shore regions and only to a smaller degree by the downfall of aerial plankton" (Norlin 1964, p. 205). In addition, although Norlin (1967) described the mechanisms by which insects may drift and be trapped on lake surfaces, his results did not give clear evidence that large lakes indeed received

comparable insect deposition to smaller ones. Likewise, his sampling design was not appropriate to infer whether there is an increase or decrease of insect biomass from shores to centers of lakes. In contrast, clear evidence for an exponential decrease of insect density with increasing distance to donor habitats comes from a study on emerging aquatic insects (Sanzone et al. 2003, whose data we used for our earlier model). Furthermore, a highly significant decay model was fitted to the declining TP concentrations in floating atmospheric deposition collectors along six transects perpendicular to the shore in the 0.15 km² Mirror Lake (New Hampshire, U.S.A.) (Cole et al. 1990). In this study, the trap content was composed of whole insects, insect parts, dust, and plant material, which mirrored the fallout of insects from nearshore vegetated zones. Whereas Cole et al.'s decay model described the TP concentrations in the traps adequately, the picture was less clear if the insect and plant parts were considered separately (Cole et al. 1990, their fig. 5), since the numerical proportions of insects in the traps were higher at 100-m and 4-m shore distance than in the traps at distances of 1, 14, and 50 m. Overall, there is not much known about the magnitude or spatial patterns of insect deposition to lakes, but a few studies suggest that the origin of insect fallouts to lakes is mainly the surrounding shoreline, such that deposition rates likely will decrease with increasing shore distance.

The two observations cited by Wurtsbaugh (2007), that the proportion of terrestrial insects in the diet composition of fish varies independently of lake size and shore distance (Wurtsbaugh et al. 1975; Ruzycki et al. 2001), are also of little help here. Fish species with a specialized insectivorous feeding strategy will always keep the proportion of insects high in their diet, even if the local availability is low, by expanding their feeding area. Conversely, feeding opportunists might be expected to feed upon diet items according to their local availability (e.g., Dörner et al. 2003). Therefore, the diet composition of individual fish caught at a certain place in the lake tells us little about the real biomasses of all potential food organisms at that place.

To validate our decay model, we calculated the insect fallout to Mirror Lake and compared the obtained insect deposition rates with those published by Cole et al. (1990). Our decay model using a medium coefficient a (50.4 mg dry wt m⁻² d⁻¹, representing the insect fallout per meter shoreline) and medium transport exponent b (0.0853 m⁻¹; see Mehner et al. 2005 for details) results in an average insect fallout of 5.7 mg dry wt m⁻² d⁻¹ for circle-shaped lakes, and 11.3 mg dry wt m⁻² d⁻¹ for more elongated (shore development factor = 2) 0.15-km² large lakes. Cole et al. (1990) estimated an average nutrient input of 11–13 μmol P m⁻² d⁻¹ for the summer months July and August. By considering that, on average, 28% of the nutrients in the traps were provided by insects (Cole et al. 1990), and that the fallout rate of insects averaged over spring, summer, and autumn is about 50% of the summer rate (Baxter et al. 2005, their table 1), the full-season average for Mirror Lake would be equivalent to about 1.68 μmol P m⁻² d⁻¹ in insect biomass. If a P concentration in insect dry weight of 0.875% is considered (see Mehner et al. 2005), the P deposition rate converts into

6.1 mg insect dry wt m⁻² d⁻¹, a value very close to our estimates. Accordingly, our decay model reliably predicted insect deposition rates empirically derived for Mirror Lake. Unfortunately, a comparison of model predictions with empirical deposition rates was not possible for the large Swedish lakes since the estimates of the amount of insects at the surface are given as areal biomasses without reference to an accumulation period or turnover time (Norlin 1964, 1967).

Do the analyses support the assumption by Wurtsbaugh (2007) that fish generally play only a small role in allochthonous nutrient subsidy or nutrient recycling in lakes? Our results confirmed that bleak feeding on terrestrial insects only marginally subsidized the nutrient pool of Lake Großer Vätersee. However, the bleak population made only a minor contribution (3.6%) to the total fish biomass (5,771 kg fresh weight km⁻²) in Lake Großer Vätersee (Mehner et al. 2005; Schulze et al. 2006), and hence a high contribution of this species to overall nutrient pools could not be expected. According to a comprehensive overview from 13 lakes, fish regenerate on average about 6% (range 0.8–22.9%) of the phosphorus produced by plankton (Griffiths 2006). Other studies have confirmed a rather high importance of fish-mediated nutrient transformation by comparing nutrient supply by fish excretion with nutrient demand of phytoplankton (overview in Vanni 2002). In particular, nutrient cycling by gizzard shad (*Dorosoma cepedianum*) supported on average 23% of phytoplankton primary production in four productive reservoirs and 8% of primary production in unproductive reservoirs with mixed-land-use watersheds in Ohio, U.S.A. (Vanni 2006; Vanni et al. 2006). In four central Minnesota (U.S.A.) wetlands, P excretion by fathead minnows (*Pimephales promelas*) supplied algal demand in the range of 38% to 124% during summer (Zimmer et al. 2006). In both species, nutrient-rich detritus formed a major part of the diet of fish, and hence fish translocated nutrients from bottom sediments to the euphotic zone, thus creating “new” phosphorus for phytoplankton production. In a similar way, “new” nutrients are supplied if fish feed in littoral zones during the day but excrete while migrating horizontally toward the pelagic zone during crepuscular and nighttime periods (Brabrand et al. 1990; Schindler et al. 1993), a behavioral pattern which is typical also for the bleak in Lake Großer Vätersee (Mehner et al. 2005; J. Ihlau unpubl. results).

Finally, fish can sequester a large amount of nutrients in body tissue (Vanni 2002; Griffiths 2006), thus making them temporarily unavailable to production. Since the diet of particular fish species can constitute, to a large part, terrestrial prey (Mehner et al. 2005; Cole et al. 2006), fish feeding on terrestrial insects can modify the temporal (and spatial, see above) scales by which allochthonous nutrients are supplied to lake phytoplankton. Nutrient storage by fish decouples the in-lake phytoplankton succession from the seasonal succession of insect fallout to lakes and provides a small, albeit continuous, supply of allochthonous nutrients by fish excretion throughout the season. Furthermore, the feeding on insects by fish, the subsequent storage of nutrients in body tissue, and the final excretion

of P by fish over the duration of the season probably provide a larger amount of allochthonous nutrients for lake phytoplankton than the amount made available by bacteria by mineralization during the short sinking period of terrestrial insects from the surface to the aphotic zone.

In conclusion, we thank Wayne Wurtsbaugh for his comments that stimulated us to refine our arguments. Whereas Wurtsbaugh's comment elucidated the low importance of fish for short-term processes at fine spatial scales such as nutrient recycling, our study placed the nutrient subsidy to lakes by insectivorous fish within the perspective of longer temporal and broader spatial scales. According to our decay model, subsidy by terrestrial fish prey is expected to be more important in very small lakes with high perimeter-to-area ratio. More empirical research is needed to verify whether the relative importance of allochthonous nutrient sources, such as insects, to lake nutrient pools indeed increases with declining system sizes. Furthermore, more experimental studies are required in order to understand the differing temporal and spatial scales at which allochthonous nutrients are processed by fish in comparison to in-lake nutrient processing by other taxa.

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