

COMMENT

Limnol. Oceanogr., 52(6), 2007, 2715–2718
© 2007, by the American Society of Limnology and Oceanography, Inc.

Nutrient cycling and transport by fish and terrestrial insect nutrient subsidies to lakes

Wayne A. Wurtsbaugh¹

Watershed Sciences Department and the Ecology Center, Utah State University, Logan, Utah 94322-5210, USA;
Velux Visiting Professor of Biodiversity, Technical University of Zurich (ETH), Swiss Federal Institute of Aquatic Science and Technology (EAWAG), Zürich, Switzerland

Mehner et al. (2005) reported that fish feeding on terrestrial insects could be important for the nutrient budgets and cycling in lakes. They studied bleak (*Alburnus alburnus*) that fed largely on terrestrial insects, and they suggested that this contributed 2.1% of the nutrient budget of a 12-ha lake (Großer Vätersee) and that the subsequent excretion by the fish was equivalent to 11% of epilimnetic dissolved phosphorus concentrations. They concluded that nutrients delivered to lakes via terrestrial insects and recycled by fish would be most important for small lakes because of the large perimeter-to-area ratio between donor and recipient habitats. Fish may have important impacts on the community structure of lakes (e.g., Brooks and Dodson 1965), and, under some circumstances, they may influence internal nutrient cycling and transport (e.g., Vanni et al. 1997, 2006). However, three aspects of Mehner et al.'s analysis may have led them to considerably overstate the influence of fish on nutrient budgets and terrestrial subsidies to lakes, regardless of the size of the system.

First, nearly all terrestrial insects consumed by fish have already fallen into the lake, so the nutrients they contain are already part of the budget. Fish feeding and excretion of nutrients could, however, speed up the movement of the new nutrients into other components of the food web. Nevertheless, the nutrients imported into the lake by insects have the potential to be recycled multiple times by bacteria, fungi, and other organisms whether fish are present or not. Nutrient recycling by fish should consequently be viewed within the context of the entire consumer community, and when so analyzed, the contribution by vertebrates is often very small (Hudson et al. 1999; Sarnelle and Knapp 2005). The relative importance of nutrient recycling by fish will be approximately proportional to their contribution to me-

tabolism, because respiration is closely tied to nutrient excretion (Brown et al. 2004). I used the sizes and abundances of the organisms in Großer Vätersee (Kasprzak et al. 2000; Adrian and Schipolowski 2003; Mehner et al. 2005) and the temperature of their habitat to estimate mass-specific respiration rates (Brown et al. 2004). This analysis indicated that the metabolism of all fish represents approximately 0.1% of total pelagic respiration, and that of bleak represents only 0.004% (Wurtsbaugh unpubl. data). Rather, bacteria and phytoplankton dominate metabolism in the water columns of lakes (Likens 1985), and consequently, most nutrients are recycled by microbes.

A second problem is that Mehner et al. (2005) compared the *annual* consumption of phosphorus in terrestrial insects by the fish to the mean total phosphorus concentration in the lake to arrive at their 2.1% contribution estimate. This comparison of a *rate* ($\text{g P L}^{-1} \text{yr}^{-1}$) with a *concentration* is inappropriate. A more appropriate comparison would have been between the total annual phosphorus budget going into the lake and that contributed by the terrestrial insects eaten by fish, but these data were not available. Mehner et al. (2005) did state that they did not find strong evidence that bleak feeding subsidized the phosphorus pool in the lake, but even the small amount they calculated was considerably overestimated. Their estimation of phosphorus excreted by fish suffers similar flaws in that they compared the *annual* rate of phosphorus excretion by fish to the mean concentration of soluble reactive phosphorus (SRP) to arrive at the 11% contribution by fish of readily utilizable nutrients. Again, comparing a rate with a concentration is problematic. When excretion rates of organisms are compared to concentrations, they are often expressed as *daily* rates of cycling. In this case, the soluble phosphorus contributed by bleak would represent only 0.03% d^{-1} of the SRP concentration in the lake. In reality, it is not even appropriate to relate phosphorus excretion by fish with the SRP because particulate phosphorus in the water column cycles within minutes to hours (Lean 1973). The more appropriate comparison of daily fish excretion rates to *total* phosphorus concentration yields an estimate of recycling by the bleak of only 0.006% d^{-1} of the phosphorus pool—this turnover rate is clearly unimportant given the overall turnover rate of this nutrient in lakes, and

¹ Corresponding author (wurts@cc.usu.edu)

Acknowledgments

Discussions with M. Vanni, C. Johnson, C. Luecke, R. Lockwood, and T. Mehner contributed substantially to the final manuscript. T. Mehner graciously provided unpublished information on fish biomasses. The work was partially supported by National Science Foundation (NSF) grant DEB 01-32983, and a Velux Foundation fellowship to the author from the Technical University of Zurich (ETH).

it is similar to their estimated contribution to community respiration.

A third limitation of the analysis was that the contribution of terrestrial insects over the lake surface may not have been correctly conceptualized. Mehner et al. (2005) did not measure insect contributions to the lake but rather based their analysis on published results of insect subsidies to streams and assumed that there would be an exponential decrease in insect deposition to the lake surface as distance from shore increased. This led them to conclude that insect contributions could only be important for fish and nutrient budgets of small lakes in forested areas with high shoreline: surface area ratios. The deposition of insects onto lake surfaces is poorly known, but Cole et al. (1990) did not find a correlation between insects falling onto a lake surface and distance from shore, suggesting that an exponential model of decreasing deposition may not be correct. Norlin (1964, 1967) suggested that most insects falling onto lake surfaces are not derived from the shoreline vegetation but rather are from "aerial plankton" that drift considerable distances from the terrestrial landscape and are deposited evenly over the lake surface in downdrafts. In large lakes, this diffuse input of "aerial plankton" trapped on the lake surface can be concentrated in downwelling zones near the shore where fish can feed on them (Norlin 1967). Consequently, terrestrial insects can be very important to fish even in large lakes. This occurs in Bear Lake, which is 280 km² and is located in the arid western United States, where terrestrial insects constitute 60% of the summer diet of juvenile cutthroat trout (*Salmo clarki utah*; Ruzycski et al. 2001). In another study, juvenile rainbow trout (*Oncorhynchus mykiss*) captured close to shore in a 0.2-km² lake ate only 15% terrestrial food, whereas larger trout that inhabited the entire lake ate 49% terrestrial insects (Wurtsbaugh et al. 1975). Thus, neither small lake sizes nor forested shorelines are necessary for terrestrial insects to be an important food source for fish.

Because fish and other vertebrates contribute only a tiny fraction of total nutrient recycling compared to that of microbes, the actual amount of recycling of nutrients by fish in Großer Vätersee or other lakes is not important. Rather, the importance of fish may be best judged by their positive or negative contribution to the nutrient budget in the water column. Indeed, as pointed out by others (Schindler and Scheuerell 2002; Vanni 2002), it is the transport of nutrients from one part of the system to another that has more influence on productivity than recycling in the water column. Fish excretion of nutrients derived from terrestrial insects represents such a subsidy, although in the case of Großer Vätersee this appears to be small. Fish nutrient transport is generally most important when they feed on or disturb benthic detrital material (Lamarra 1975; Brabrand, et al. 1990; Schaus et al. 1997; Vanni et al. 1997; Vanni 2002) because the upper few centimeters of lake sediments contain an order of magnitude more nutrients than the overlying water (Wetzel 2001). Fish can also be relatively important in nutrient cycling under special conditions when other recyclers such as zooplankton have been depressed by stocking of planktivorous fish and rotenone treatments (Schindler et

al. 1993) or when they become extremely abundant when piscivores are absent (Zimmer et al. 2006).

It is important to recognize that although fish (or zooplankton) can transport nutrients into the pelagic zone, this effect can be offset by two processes that decrease nutrients in the water column. First, fish store limiting nutrients in their bodies, making them unavailable for phytoplankton (Kraft 1992). Secondly, fish, and particularly zooplankton, may export nutrients from the mixed layer via defecation (Kraft 1992; Pilati and Wurtsbaugh 2003; but see Sarnelle 1999), again making them unavailable to phytoplankton in the photic zone. A recent study by Glaholt and Vanni (2005) demonstrated that these two processes counterbalance the effects of nutrient excretion by fish in the water column and provide for the net transport of nutrients into the sediments of mesocosms. Consequently, the fish in their experiment had no significant effect on phytoplankton abundance (seston P), but they did increase the amount of phosphorus in the periphyton community. Similarly, although marine zooplankton and fish recycle nutrients in the water column and thus support recycled primary production (sensu Caraco et al. 1992), their net effect is to export nutrients from the mixed layer and thus reduce the phytoplankton in the water column (Turner 2002). Consequently, when considering how fish influence nutrient balance in the water columns of lakes, it is important to consider their *net* effect on the transport of nutrients among the pelagic, benthic, and littoral zones.

Fish, however, are not the only vectors of nutrient transport between the littoral and benthic zones and the open water. The metabolism of benthic organisms (microbes and others) is much greater than pelagic respiration (Wetzel 2001), and in small and moderate size lakes, a considerable portion of the epilimnion is in contact with the sediments (e.g. 46% in Großer Vätersee; Kasprzak et al. 2000). When metabolic processes release nutrients, a portion of these can be swept into the open waters of a lake because horizontal diffusivity is very high. For example, a grazing insect near the shore or decomposition of a dead terrestrial insect in the littoral sediments will release nutrients into the water and a portion of these can be advected to the pelagic zone, although a large portion would be recaptured by the biofilm community (Axler and Rueter 1996). Likewise, wave action can release nutrients recycled by microbes in the sediments and transport them throughout the lake (Precht and Huettel 2003). The relative importance of these different transport processes for epilimnetic production has not been studied, but it is clear that fish are not the only vectors transporting nutrients between different areas of a lake. Given the large discrepancy between the metabolism of insectivorous fishes and that of other components of the ecosystem, we can hypothesize that the fish would be responsible for only a small component of this transfer.

Although terrestrial insects are not likely to be an important subsidy to nutrient budgets of lakes under most circumstances, they can be very important for particular species of fish that feed on them, regardless of the size of the lake or the proximity of fish to the shore. Indeed,

Mehner et al. (2005) found that terrestrial insects contributed 73% of the diet of bleak in the small, 0.12-km² lake they studied. If fish abundance is enhanced by this subsidy, then their subsequent predation on zooplankton and other prey could affect nutrient recycling by these organisms. Thus, although direct effects of feeding on insects and subsequent excretion are likely minimal, there could be other indirect effects that influence nutrient cycling in lakes.

The importance of nutrient and organic matter subsidies to lakes has been studied for decades, and there is growing interest in this area. Inorganic nutrient flow from watersheds to lakes has been studied extensively (e.g., Prepas et al. 2001), and recent work has shown that organic matter subsidies can also be important (Pace et al. 2004). When subsidies are analyzed, however, it is crucial that appropriate metrics are utilized. It is inappropriate, for example, to compare the nutrient contribution of external organisms like insects and salmon (e.g., Thomas et al. 2003; Mehner et al. 2005) to only the SRP or NO₃ in a stream or lake, because those dissolved inorganic fractions often constitute only a small fraction of the total nutrients cycling through the system. The magnitude of the subsidized area must also be taken into account. If insects emerging from streams or decomposing salmon fertilize narrow riparian corridors, it is important to remember that these corridors represent, at most, a few percent of the overall watershed that is contributing nutrients to a stream. Hence, terrestrial subsidies can be very important to particular species (e.g., bleak), or of localized importance to bordering communities, but they likely have limited impacts on lake or watershed nutrient budgets.

The relative importance of subsidies to the neuston of lakes is an understudied aspect of limnology, and the research conducted by Mehner et al. (2005) highlights the processes involved. Future work, however, will require careful measurements and analyses of these processes in order to determine just how important they are for lake ecosystems.

References

- ADRIAN, R., AND T. SCHIPOLOWSKI. 2003. Bacterial and protozoan mass accumulation in the deep chlorophyll maximum of a mesotrophic lake. *Archiv. für Hydrobiol.* **157**: 27–46.
- AXLER, R. P., AND J. E. REUTER. 1996. Nitrate uptake by phytoplankton and periphyton: Whole-lake enrichments and mesocosm-N-15 experiments in an oligotrophic lake. *Limnol. Oceanogr.* **41**: 659–671.
- BRABRAND, A., B. A. FAAFENG, AND J. P. M. NILSSEN. 1990. Relative importance of phosphorus supply to phytoplankton production: Fish excretion versus external loading. *Can. J. Fish. Aquat. Sci.* **47**: 364–372.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* **150**: 28–35.
- BROWN, J. H., J. F. GILLOOLY, A. P. ALLEN, V. M. SAVAGE, AND G. B. WEST. 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789.
- CARACO, N. F., J. J. COLE, AND G. E. LIKENS. 1992. New and recycled primary production in an oligotrophic lake: Insights for summer phosphorus dynamics. *Limnol. Oceanogr.* **37**: 590–602.
- COLE, J. J., N. F. CARACO, AND G. E. LIKENS. 1990. Short-range atmospheric transport: A significant source of phosphorus to an oligotrophic lake. *Limnol. Oceanogr.* **35**: 1230–1237.
- GLAHOLT, S. P., JR., AND M. J. VANNI. 2005. Ecological responses to simulated benthic-derived nutrient subsidies mediated by omnivorous fish. *Freshwater Biol.* **50**: 1864–1881.
- HUDSON, J. J., W. D. TAYLOR, AND D. W. SCHINDLER. 1999. Planktonic nutrient regeneration and cycling efficiency in temperate lakes. *Nature* **400**: 659–661.
- KASPRZAK, P., F. GERVAIS, R. ADRIAN, W. WEILER, R. RADKE, I. JÄGER, S. RIEST, U. SIEDEL, B. SCHNEIDER, M. BÖHME, R. ECKMANN, AND N. WALZ. 2000. Trophic characterization, pelagic food web structure and comparison of two mesotrophic lakes in Brandenburg (Germany). *Int. Rev. Hydrobiol.* **85**: 167–189.
- KRAFT, C. E. 1992. Estimates of phosphorus cycling by fishes using a bioenergetics model. *Can. J. Fish. Aquat. Sci.* **49**: 2596–2604.
- LAMARRA, V. A., AND JR. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. *Verh. Int. Verein. Limnol.* **19**: 2461–2468.
- LEAN, D. R. S. 1973. Phosphorus dynamics in lake water. *Science* **179**: 678–680.
- LIKENS, G. E. [ED.]. 1985. An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.
- MEHNER, T., J. IHLAU, H. DÖRNER, AND F. HÖLKER. 2005. Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes? *Limnol. Oceanogr.* **50**: 2022–2031.
- NORLIN, Å. 1964. The occurrence of terrestrial insects on the surface of two lakes in northern Sweden (Ankarvattnet and Blåsjön). *Rep. Inst. Freshwater Res. Drottningholm* **45**: 196–205.
- . 1967. Terrestrial insects on lake surfaces, their availability and importance as fish food. *Rep. Inst. Freshwater Res. Drottningholm* **47**: 39–55.
- PACE, M. L., J. J. COLE, S. R. CARPENTER, J. F. KITCHELL, J. R. HODGSON, M. VAN DE BOGERT, D. L. BLADE, E. S. KRITZBERG, AND D. BASTVIKEN. 2004. Whole-lake carbon-13 additions reveal terrestrial support for aquatic food webs. *Nature* **427**: 240–243.
- PILATI, A., AND W. A. WURTSBAUGH. 2003. Importance of zooplankton for the persistence of a deep chlorophyll layer: A limnocorral experiment. *Limnol. Oceanogr.* **48**: 249–260.
- PRECHT, E., AND M. HUETTEL. 2003. Advective pore-water exchange driven by surface gravity waves and its ecological implications. *Limnol. Oceanogr.* **48**: 1674–1684.
- PREPAS, E. E., D. PLANAS, J. J. GIBSON, D. H. VITT, T. D. PROWSE, W. P. DINSMORE, L. A. HALSEY, P. M. MCEACHERN, S. PAQUET, G. J. SCRIMGEOUR, W. M. TONN, C. A. PASZKOWSKI, AND K. WOLFSTEIN. 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: A comparison of wetland- and upland-dominated catchments. *Can. J. Fish. Aquat. Sci.* **58**: 1286–1299.
- RUZYCKI, J. R., W. A. WURTSBAUGH, AND C. LUECKE. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah-Idaho. *Trans. Am. Fish. Soc.* **130**: 1175–1189.
- SARNELLE, O. 1999. Zooplankton effects on vertical particulate flux: Testable models and experimental results. *Limnol. Oceanogr.* **44**: 357–370.
- , AND R. A. KNAPP. 2005. Nutrient recycling by fish versus zooplankton grazing as drivers of the trophic cascade in alpine lakes. *Limnol. Oceanogr.* **50**: 2032–2042.

- SCHAUS, M. H., M. J. VANNI, T. E. WISSING, M. T. BREMIGAN, J. E. GARVEY, AND R. A. STEIN. 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnol. Oceanogr.* **41**: 1386–1397.
- SCHINDLER, D. E., J. F. KITCHELL, S. HE, S. R. CARPENTER, J. R. HODGSON, AND K. L. COTTINGHAM. 1993. Food-web structure and phosphorus cycling in lakes. *Trans. Am. Fish. Soc.* **122**: 756–772.
- , AND M. D. SCHEUERELL. 2002. Habitat coupling in lake ecosystems. *Oikos* **98**: 177–189.
- THOMAS, S. A., T. V. ROYER, AND G. W. MINSHALL. 2003. Assessing the historic contribution of marine-derived nutrients to Idaho streams. *Am. Fish. Soc. Symp.* **34**: 41–55.
- TURNER, J. T. 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.* **27**: 57–102.
- VANNI, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Ann. Rev. Ecol. Systematics* **33**: 341–370.
- , A. M. BOWLING, E. M. DICKMAN, R. S. HALE, K. A. HIGGINS, M. J. HORGAN, L. B. KNOLL, W. H. RENWICK, AND R. A. STEIN. 2006. Nutrient cycling by fish supports relatively more primary production as lake productivity increases. *Ecology* **87**: 1696–1709.
- , C. D. LAYNE, AND S. E. ARNOTT. 1997. “Top-down” trophic interactions in lakes: Effects of fish on nutrient dynamics. *Ecology* **78**: 1–20.
- WETZEL, R. G. 2001. *Limnology. Lake and River Ecosystems*. 3rd ed., Academic Press.
- WURTSBAUGH, W. A., R. W. BROCKSEN, AND C. R. GOLDMAN. 1975. Food and distribution of underyearling brook and rainbow trout in Castle Lake, California. *Trans. Am. Fish. Soc.* **104**: 88–95.
- ZIMMER, K. D., B. R. HERWIG, AND L. M. LAURICH. 2006. Nutrient excretion by fish in wetland ecosystems and its potential to support algal production. *Limnol. Oceanogr.* **51**: 197–207.

Received: 9 December 2005

Amended: 24 November 2006

Accepted: 25 November 2006