

NUTRIENT CYCLING BY ANIMALS IN FRESHWATER ECOSYSTEMS

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Key Words lakes, nitrogen, nutrient excretion, phosphorus, streams

■ **Abstract** Animals are important in nutrient cycling in freshwater ecosystems. Via excretory processes, animals can supply nutrients (nitrogen and phosphorus) at rates comparable to major nutrient sources, and nutrient cycling by animals can support a substantial proportion of the nutrient demands of primary producers. In addition, animals may exert strong impacts on the species composition of primary producers via effects on nutrient supply rates and ratios. Animals can either recycle nutrients within a habitat, or translocate nutrients across habitats or ecosystems. Nutrient translocation by relatively large animals may be particularly important for stimulating new primary production and for increasing nutrient standing stocks in recipient habitats. Animals also have numerous indirect effects on nutrient fluxes via effects on their prey or by modification of the physical environment. Future studies must quantify how the importance of animal-mediated nutrient cycling varies among taxa and along environmental gradients such as ecosystem size and productivity.

INTRODUCTION

The cycling of nutrients is critical for the sustenance of ecosystems (DeAngelis et al. 1989, DeAngelis 1992, Costanza et al. 1997, Chapin et al. 2000). Nutrient cycling may be defined as the transformation of nutrients from one chemical form to another, and/or the flux of nutrients between organisms, habitats, or ecosystems. In most ecosystems, microbes (bacteria and fungi) are important agents of nutrient cycling (Schlesinger 1997). Nutrient inputs from outside ecosystem boundaries (often referred to as allochthonous inputs) are also important in many ecosystems (Polis et al. 1997, Carpenter et al. 1998). However, over the past three decades, ecologists have shown that animals can be important in the cycling of nutrients in terrestrial, marine, and freshwater ecosystems (e.g., Kitchell et al. 1979; Meyer & Schultz 1985; Grimm 1988a,b; Pastor et al. 1993; Vanni 1996; McNaughton et al. 1997; Vanni et al. 1997; Sirotnak & Huntly 2000; Hjerne & Hansson 2002). In most aquatic ecosystems, attention has focused on the cycling of nitrogen (N) and phosphorus (P) because they are the nutrients most likely to limit primary

producers and perhaps heterotrophic microbes (Pace & Funke 1991, Suberkropp & Chauvet 1995, Smith 1998, Rosemond et al. 2002).

Animals have many strong effects on aquatic food webs and ecosystems, and it is necessary to place the role of animal-mediated nutrient cycling within this context. Predators such as fish can directly or indirectly control the biomass and species composition of trophic levels below them. One of the most well-studied effects is the trophic cascade (e.g., Carpenter et al. 1985), whereby predation by fish results in reduced biomass and altered species composition of herbivores, and in increased biomass and altered species composition of primary producers (usually algae). Several studies have shown that the trophic cascade also affects nutrient concentrations, the relative apportionment of nutrients to different ecosystem pools, and the extent and severity of nutrient limitation (e.g., Shapiro & Wright 1984, Andersson et al. 1988, Elser et al. 1988, Mazumder et al. 1989, Reinertsen et al. 1990, Carpenter et al. 1992, Rosemond 1993, Rosemond et al. 1993, Vanni et al. 1997, Drenner et al. 1998, Elser et al. 2000). These studies and others show that the increase in primary producers set in motion by carnivores cannot be completely explained by a reduction in herbivory, and they suggest that changes in nutrient cycling may at least partly explain the trophic cascade response of primary producers. Indeed, in referring to P-limited lakes, Carpenter et al. (1992) suggest that "changes in trophic structure that derive from trophic cascades can be viewed as changes in the phosphorus cycle driven by fishes."

Freshwater animals can affect nutrient cycling in many ways (Figure 1), which can be characterized as direct and indirect. I consider their direct effects to be those that emanate from the physiological transformation of nutrients from one form to another within their own bodies. This includes consumption of nutrients and their subsequent allocation to feces, growth, and nutrient excretion (Figure 1). Indirect effects occur when animals affect nutrient fluxes through impacts on their prey and/or on physical habitat structure (Figure 1). In this review I first consider direct effects animals have on nutrient cycling, starting with processes at the level of individual animals and then proceeding to effects on communities and ecosystems. Then I consider the indirect effects animals have on nutrients.

NUTRIENT CYCLING AT THE INDIVIDUAL LEVEL

Nutrient Mass Balance

The amount of nutrients ingested and released by an animal must follow principles of mass balance. Nutrients that are ingested but not assimilated through an animal's gut wall are released as feces, a process referred to as nutrient egestion. Fecal nutrients are not usually directly available to primary producers, which require nutrients in dissolved form. However, fecal nutrients may subsequently become available to primary producers via decomposition and remineralization by microbes (e.g., Hansson et al. 1987). Assimilated nutrients have two fates: They can be sequestered into animal tissues via growth, in which case the nutrients are

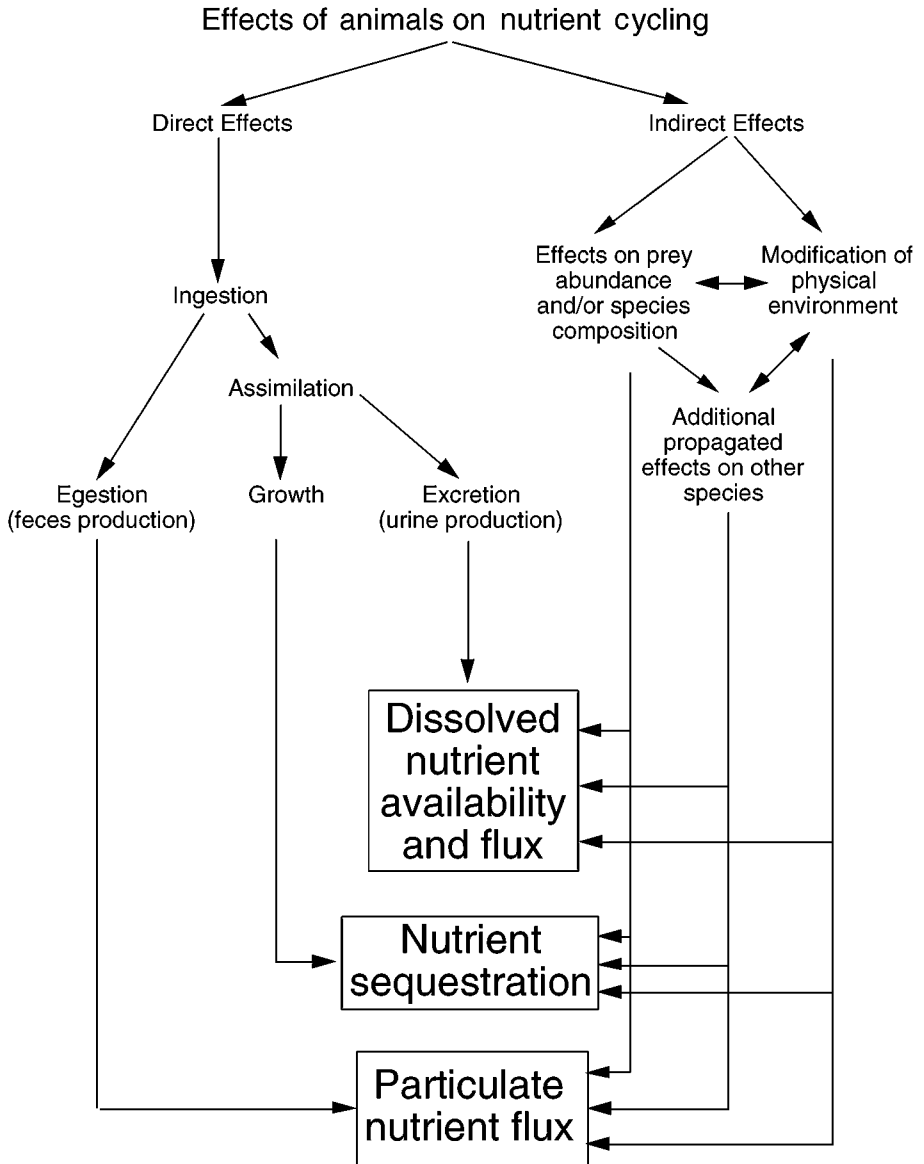


Figure 1 Schematic diagram of animal-mediated nutrient cycling via direct and indirect pathways.

not immediately available to other organisms; alternatively, they are released in dissolved form through kidneys or functionally similar organs, a process known as nutrient excretion.

Nutrient excretion is the most direct means by which animals can provide nutrients for primary producers (algae and vascular plants) and heterotrophic microbes (bacteria and fungi). Although some freshwater animals excrete certain nutrients in organic form (e.g., urea), most N and P is excreted in inorganic forms (e.g., ammonia, phosphate). Thus the rates at which animals excrete N and P are potentially important for primary producers and heterotrophic microbes. In addition, because either N or P can be limiting, the ratio at which animals excrete these nutrients (hereafter excretion N:P) is potentially important in determining the relative degree of N vs. P limitation (Elser et al. 1988, Sterner 1990, Sterner & Elser 2002) and algal species composition (Tilman et al. 1982, Smith 1983).

Nutrient Recycling versus Nutrient Translocation

Nutrient cycling through an animal's body can be divided into two functionally distinct processes: nutrient recycling and nutrient translocation. Nutrient recycling occurs when an animal releases nutrients within the same habitat in which food was ingested. For example, when zooplankton consume phytoplankton in the open water of a lake and excrete nutrients back into the water, they recycle nutrients already in that habitat. In contrast, nutrient translocation (or transport) refers to the process by which an animal physically moves nutrients between habitats or ecosystems, often accompanied by transformation of nutrients from one chemical form to another (Kitchell et al. 1979, Shapiro & Carlson 1982, Vanni 1996). For example, when an animal feeds on benthic prey and excretes nutrients into the water, it translocates nutrients from benthic to pelagic habitats and converts nutrients from particulate to dissolved forms. In this case, animals move nutrients between habitats within a single ecosystem, but nutrient translocation can also occur between different ecosystems, often at great spatial and temporal scales.

What makes nutrient translocation different from recycling is that in the former, nutrients are moved across physical boundaries or against physical processes that impede nutrient movement. Such impediments include the sediment-water interface, the thermocline that separates surface and deep water layers, and the downstream flow of water. In many aquatic systems, primary producers cannot utilize nutrients in deep waters because of inadequate light. Therefore, any process that brings nutrients to the euphotic zone (surface waters where light intensity is sufficient for photosynthesis) is potentially important. Nutrients delivered to the euphotic zone from deeper waters, littoral/benthic areas, or outside the ecosystem are often referred to as "new" nutrients (Dugdale & Goering 1967, Eppley & Peterson 1979, Caraco et al. 1992) because these nutrients have been recently translocated from another habitat or ecosystem. New (translocated) nutrients can stimulate "new primary production" (Dugdale & Goering 1967, Eppley &

Peterson 1979, Caraco et al. 1992, Vanni 1996) and increase the total mass of nutrients in the recipient habitat or ecosystem. In contrast, nutrient recycling cannot directly increase the mass of nutrients in a habitat or ecosystem, but rather it sustains "recycled production." The implications of whether animals recycle or translocate nutrients are considerable and are discussed throughout this review.

Measurement of Excretion Rates

Excretion rates can be estimated by using bioenergetics/mass balance models or by direct measurement. In the former approach, excretion rate is estimated as nutrients ingested minus nutrients allocated to egestion and growth (e.g., Kraft 1992, Schindler et al. 1993). Direct measurement usually entails capturing animals in the field and placing them in containers in which the accumulation of nutrients is quantified. Both methods have their advantages and disadvantages, but limited comparative data suggest that they yield similar excretion rates and ratios for fish (Mather et al. 1995, Vanni 1996, Schindler & Eby 1997, Hood 2000, Vanni et al. 2002). Therefore I treat rates obtained by both methods equally. However, many early attempts to measure excretion rates in the field used relatively long incubation times (length of time an animal is held without food after collection). This leads to underestimation of rates because animals are held without food during incubations, and excretion rates decline quickly after feeding ceases (Lehman 1980a, Devine & Vanni 2002). Therefore, I do not consider studies with long incubation times in evaluating nutrient excretion rates in nature.

FACTORS MEDIATING NUTRIENT EXCRETION BY ANIMALS

Body Size

Because of allometric constraints on metabolism (Peters 1983), mass-specific nutrient excretion rates of animals (i.e., nutrients excreted per unit body mass per unit time) usually decline with increasing body mass. Much of the evidence for allometric relationships derives from laboratory studies, in which animals were either not fed or fed a controlled ration, or from field studies with relatively long incubation times. These studies yield excretion rates that are not necessarily indicative of those in nature. Nevertheless, they show convincing allometric effects for fish (e.g., Gerking 1955), zooplankton (e.g., Wen & Peters 1994), and benthic invertebrates (e.g., Lauritsen & Mosley 1989), as do many field studies (Brabrand et al. 1990, Schaus et al. 1997, Davis et al. 2000, Gido 2002).

Temperature

Nutrient excretion rates of aquatic animals also increase with temperature due to the dependence of metabolic rates on temperature. Estimates of Q_{10} (i.e., the

factor by which a rate increases for every 10°C increase in temperature) for nutrient excretion rates of animals are similar to Q_{10} values for other metabolic processes, and such values are generally between 1.5 and 2.5 (e.g., Gardner et al. 1981, Wen & Peters 1994, Schaus et al. 1997, Devine & Vanni 2002).

Ecological Stoichiometry: Body and Food Nutrient Composition

THEORY Because nutrient excretion is constrained by mass balance, rates must be affected by the nutrient composition of the animal's body and its food (Olsen et al. 1986, Sterner 1990, Sterner et al. 1992, Elser & Urabe 1999, Sterner & Elser 2002). Ecological stoichiometry theory proposes that individual animal species maintain relatively constant body nutrient contents per unit body mass. Thus, during growth, an animal will incorporate nutrients at a rate needed to maintain constant body nutrient composition and will excrete nutrients that are assimilated but not needed for growth. Therefore, an animal feeding on a nutrient-rich food source will excrete more nutrients than one feeding on a nutrient-poor source, all else being equal. Similarly, an animal with a relatively low nutrient content in its body will allocate fewer nutrients to growth and will hence excrete more nutrients than an animal with a high body nutrient composition. Stoichiometry theory also predicts that the excretion N:P of animals is a function of the imbalance between the N:P ratios in its body and its food. An individual with a low body N:P ratio should release nutrients at a relatively high N:P ratio compared to an individual with a high body N:P ratio, if the two are feeding on the same food. More generally, the N:P ratio released by an animal should be negatively correlated with the N:P of its body tissues and positively correlated with the N:P of its food.

EVIDENCE Relatively few field studies have explicitly tested the hypothesis that nutrient excretion rates are functions of the nutrient composition of animals and their food. Elser & Urabe (1999) suggested that for herbivorous zooplankton, food N:P is more important than body N:P in determining excretion N:P, perhaps because the N:P of their food (phytoplankton) is much more variable than the N:P of zooplankton body tissues. Schindler & Eby (1997) used bioenergetics/mass balance models to show that the excretion N:P of 18 species of fish is relatively invariant and low (generally <15:1 molar) as long as fish growth is not limited by P. The excretion N:P can be much higher if fish growth is limited by P because fish need to sequester a greater proportion of assimilated P, but fish growth rates are apparently rarely limited by P (Schindler & Eby 1997). Similarly, Sterner & George (2000) showed that four species of cyprinid fish (minnows) differed only slightly in body N and P contents and assimilation rates, and by implication, excretion rates of these species were probably similar.

In contrast, Vanni et al. (2002) found > tenfold variation in excretion rates and ratios among 26 fish and 2 amphibian species in a tropical stream in Venezuela, and ecological stoichiometry explained much of this variation (body size was

important also). Mass-specific P excretion rate was negatively correlated with body P content, and excretion N:P was negatively correlated with body N:P, as predicted by stoichiometry theory. Body nutrient content may have had a greater effect on excretion rates and ratios than in other studies because of relatively large interspecific variation in body P content. Some fish, particularly the armored catfish (Loricariidae), have very high P contents in their bodies compared to other taxa, apparently because they need to sequester P to make their armor, which is modified bone (Vanni et al. 2002). Loricariids excrete P at very low rates and have high excretion N:P ratios. The relative abundance of loricariids in neotropical streams (Lowe-McConnell 1987, Power 1990) may be very important in determining variation among taxa in excretion rates and ratios.

IMPORTANCE OF NUTRIENT EXCRETION BY ANIMALS FOR COMMUNITIES AND ECOSYSTEMS

Approaches to Quantifying the Importance of Nutrient Excretion by Animals

There are three basic approaches to estimating the importance of animal-mediated nutrient excretion. One is to compare animals' nutrient excretion rates to the rates at which nutrients are supplied by other sources. While this may seem straightforward, in reality it is often very difficult to quantify, and sometimes even to identify, all nutrient fluxes in an ecosystem (e.g., Caraco et al. 1992). Therefore, nutrient excretion by animals is often compared to other sources known to be important in many ecosystems, such as inputs from watersheds and release of nutrients from sediments via microbial processes.

An alternative, or surrogate, approach is to compare nutrient excretion rates by animals to nutrient demand by producers in the ecosystem. If nutrient excretion by animals supports a substantial proportion of nutrient demand, it can be concluded that animals are important in overall nutrient supply, without actually measuring other nutrient fluxes. Nutrient demand is often estimated as the rate at which primary producers utilize nutrients (e.g., Grimm 1988a,b; Schindler et al. 1993). However, this may underestimate total ecosystem demand because heterotrophic microbes also utilize, and may compete with algae for, limiting nutrients (e.g., Sterner et al. 1995, Suberkropp & Chauvet 1995). One assumption behind the supply/demand approach is that total nutrient demand equals nutrient supply from all sources; therefore the proportion of demand supported by any one source can be equated with the proportion of total nutrients supplied. This approach is valid only for the limiting nutrient because the total supply rate of a nonlimiting nutrient may be much higher than demand for that nutrient.

The third way to evaluate the importance of nutrient excretion by animals is to experimentally isolate and quantify the effects of nutrient excretion on recipients of nutrients (primary producers or heterotrophic microbes). This approach seeks mainly to quantify population- or community-level effects, and it involves

experimentally separating effects of consumption and excretion for the animals in question.

Evidence for the Importance of Nutrient Excretion by Animals: Nutrient Supply and Demand Studies

Small animals such as zooplankton are well known as an important potential source of nutrients in lakes and oceans. The role of larger animals such as fish is less clear, and some investigators have argued that large animals play only a minor role in supplying nutrients compared to small animals (e.g., Nakashima & Leggett 1980, Hudson et al. 1999). This may seem logical because large animals excrete nutrients at lower mass-specific rates and often have lower population biomass than do small animals. However, the biomass of large animals can sometimes be quite high, and the available data suggest that ecosystem-wide excretion rates of large animals can be as high as those of small animals (Table 1). In addition, because of greater mobility, large animals are more likely than small animals to translocate nutrients (Vanni 1996). Because body size has been considered a possible mediating factor in regulating nutrient cycling rates, I have organized this section according to body size.

ZOOPLANKTON For decades, ecologists have realized that nutrient excretion by zooplankton can be important in sustaining primary production in lakes and in the sea (Barlow & Bishop 1965, Goldman et al. 1979, Lehman 1980a, Lehman & Sandgren 1985, Sterner 1989). Unfortunately, many early estimates of nutrient excretion by zooplankton may have produced biased rates due to methodological problems (as discussed by Lehman 1980a,b), and on a per-mass basis, nutrient excretion rates vary greatly among studies (e.g., Lehman 1980b, Gulati et al. 1995). Nevertheless, recent estimates using refined methods suggest that excretion by zooplankton can supply substantial amounts of nutrients and support a substantial fraction of phytoplankton primary production (Table 1). In many lakes, nutrient excretion by zooplankton represents mostly recycled nutrients, rather than translocated nutrients, because zooplankton feed and excrete in the euphotic zone. Zooplankton can undergo daily vertical migrations and, in the process, translocate nutrients between deep water and the euphotic zone. However, the net effect of vertical migration is probably a loss of nutrients from the euphotic zone because zooplankton feed and excrete there, but usually do not feed (but excrete) in deeper waters (Wright & Shapiro 1984).

BENTHIC INVERTEBRATES Nutrient excretion by benthic invertebrates can also be important in lakes and streams (Table 1; Gardner et al. 1981, Grimm 1988a, Arnott & Vanni 1996, Devine & Vanni 2002). For example, benthic insects and snails supplied 15% to 70% of algal N demand in a desert stream (Grimm 1988a), and P excretion by unionid mussels exceeded direct P release from sediments in a mesotrophic lake (Nalepa et al. 1991). Benthic invertebrates can either recycle or translocate nutrients. Burrowing invertebrates (e.g., chironomids, worms) mostly

TABLE 1 N and P excretion rates and excretion N:P of various animals, and the percentage of primary producer N and P demand supported by excretion

Lake or stream	Taxonomic identity	N excretion rate ^a (mg N/m ² /d)	P excretion rate ^a (mg P/m ² /d)	Excretion N:P ^a (molar)	N demand supported ^a (%)	P demand supported ^a (%)	Source
Zooplankton							
Lake Washington	Assemblage ^b	20.5	4.00	13	24	33	Lehman 1980b
Castle Lake	Assemblage	10.9 (1.5–24.5)			57 (6–160)		Axler et al. 1981
Lake Tahoe	Assemblage				0.5		Carney & Elser 1990
Lake Titicaca	Assemblage				11.5		Carney & Elser 1990
Lake Michigan	Assemblage					58	Carney & Elser 1990
Latvian lakes (8 lakes), May–Oct	Assemblage		3.03 (0.69–4.99)			16 (2–34)	Gutelmacher and Makartseva 1990
Latvian lakes (8 lakes), winter	Assemblage		0.05 (0.01–0.12)				Gutelmacher & Makartseva 1990
West Long Lake	Assemblage		0.83			26	Schindler et al. 1993
Peter Lake	Assemblage		0.16			4	Schindler et al. 1993
Lake Biwa	Assemblage	1.4–11.7	0.07–0.61	19–23	43 (3–104)	15 (1–36)	Urabe et al. 1995
Lake Pend Oreille	Opposum shrimp (<i>Mysis relicta</i>)		0.07				Chippis & Bennett 2000
Benthic invertebrates							
Sycamore Creek	Insects and snails	85.0 (33.0–137.0)	0.16		15–70		Grimm 1988a
Lake St. Clair	<i>Lampsilis radiata siliquidea</i> (unionid)						Nalepa et al. 1991
Lake Suwa	Dipterans, tubificids		1.20				Fukuhara & Yasuda 1985
Lake Erie, western basin	Zebra mussel (<i>Dreissena polymorpha</i>)	222.3	58.50	8 (3–18)			Arnott & Vanni 1996
Snowflake Lake	<i>Gammarus lacustris</i> (amphipod)		1.11				Wilhelm et al. 1999
Acton Lake	Dipterans, tubificids	10.8	1.45	16	8	10	Devine & Vanni 2002; Knoll et al. in review
Fish							
Sycamore Creek	Longfin dace (<i>Agosia chrysogaster</i>)	19.1 (13.2–24.9)			5–10		Grimm 1988b
Rio Las Marías	Assemblage	63.9	7.17	20	49	126	Hood 2000, Vanni et al. 2002

(Continued)

TABLE 1 (Continued)

Lake or stream	Taxonomic identity	N excretion rate ^a (mg N/m ² /d)	P excretion rate ^a (mg P/m ² /d)	Excretion N:P ^b (molar)	N demand supported ^a (%)	P demand supported ^a (%)	Source
Lake Gjersjøen (May–Oct)	Roach (<i>Rutilus rutilus</i>)	1.21					Brabrand et al. 1990
Lake Gjersjøen (June–July)	Roach (<i>Rutilus rutilus</i>)	2.95					Brabrand et al. 1990
Lake Memphremagog	Young-of-year Yellow perch (<i>Perca flavescens</i>)	3.5–7.4	0.35–2.07	13–47			Kraft 1992
Lake Michigan ^c	Alewife (<i>Alosa pseudoharengus</i>)	2.19					Kraft 1993
West Long Lake	Assemblage	0.15				5	Schindler et al. 1993
Peter Lake	Assemblage	2.30				36	Schindler et al. 1993
Lake Finjasjön	Roach (<i>Rutilus rutilus</i>), Bream (<i>Abramis brama</i>)	0.53					Persson 1997a
Acton Lake	Gizzard shad (<i>Dorosoma cepedianum</i>)	35.3	5.46	17	25	36	Schaus et al. 1997, Knoll et al. in review
Bautzen Reservoir	Young-of-year fish		0.01–0.05				Mehner et al. 1998
Lake Pend Oreille	Kokanee salmon (<i>Oncorhynchus nerka</i>)	0.02					Chippis & Bennett 2000
Sierra Nevada lakes (5 lakes, stocked)	Trout	0.02					Schindler et al. 2001
Sierra Nevada lakes (7 lakes, unstocked)	Trout		0.01				Schindler et al. 2001
Lake Texoma	Benthivorous fish assemblage	35.0	1.00	82			Gido 2002
Birds							
Bosque del Apache wetland ^d	Lesser snow geese (<i>Chen caerulescens caerulescens</i>)	43.1	5.42	18			Post et al. 1998

^aValues outside parentheses are means, whereas those in parentheses are ranges.

^bAssemblage means that parameters were quantified for the entire assemblage (all taxa) within that group.

^cIncludes P egestion as well as excretion.

^dIncludes only new nutrients, i.e., nutrients translocated from outside the wetland.

consume benthic food and translocate nutrients into the water column. In contrast, taxa such as unionid and zebra mussels, which filter phytoplankton from the water column, mostly recycle nutrients (Nalepa et al. 1991, Arnott & Vanni 1996). Note that many earlier studies may have underestimated excretion rates of benthic invertebrates because incubation times were too long, thus producing rates not reflective of natural feeding conditions (Devine & Vanni 2002).

FISH Several recent studies show the importance of nutrient excretion by fish (Table 1). Nutrient excretion rates of fish assemblages can be comparable to, or exceed, nutrient input rates from external sources in lakes (inflow streams: Brabrand et al. 1990, Persson 1997a; atmosphere: Schindler et al. 2001) and can support a substantial fraction of algal nutrient demand in lakes (Schindler et al. 1993) and streams (Grimm 1988b, Hood 2000, Vanni et al. 2002). P excretion rates of fish can exceed watershed inputs even in reservoirs that are located in highly agricultural watersheds and thus receive large quantities of allochthonous nutrients (Schaus et al. 1997, Vanni et al. 2001). However, the importance of fish may be most pronounced during dry periods when external inputs are reduced (Gido 2002). In many lakes, most nutrients excreted by fish are derived from benthic/littoral food sources, indicating that fish translocate nutrients to pelagic habitats (Brabrand et al. 1990; Schindler et al. 1993, 2001; Schaus et al. 1997; Gido 2002). Even fish referred to as “planktivores” often rely heavily on littoral/benthic prey (Schindler et al. 1993). In contrast, Kraft (1992, 1993) and Persson (1997a) found that fish fed mainly on plankton and thus provided primarily recycled nutrients. The extent to which fish provide new or recycled nutrients will depend on fish species as well as variation in diet, which can be great even within a species. Stable isotope studies show that most freshwater fish obtain a substantial fraction of their food from benthic sources (Hecky & Hesslein 1995, Schindler & Scheuerell 2002), so in many ecosystems, a substantial proportion of nutrients excreted by fish are likely to be translocated from benthic to pelagic habitats.

The relative roles of different animal taxa in nutrient cycling are likely to depend on food web configuration. For example, Schindler et al. (1993) found that fish and zooplankton provided 5% and 26%, respectively, of phytoplankton P demand in a lake dominated by piscivorous fish and with few small fish. However, in a lake dominated by small fish (which fed mostly on littoral prey but also zooplankton), nutrient excretion by fish supported 36% of P demand by phytoplankton, and excretion by zooplankton supported only 4% (Schindler et al. 1993). Fish were more important in the latter lake because small fish suppress zooplankton populations, rendering their excretion less important, and because small fish have much higher mass-specific excretion rates than piscivores (Schindler et al. 1993). Interestingly, primary production was about 30% higher in the lake with small fish, corresponding to a 40% higher excretion rate by fish and zooplankton combined.

EXCRETION N:P Surprisingly few field studies have quantified excretion N:P and its impacts on nutrient recipients. Seasonal or interannual increases in *Daphnia*

are associated with more severe P limitation and less severe N limitation of phytoplankton (Elser et al. 1988, 2000; Urabe et al. 1995; MacKay & Elser 1998), presumably because *Daphnia* excretes nutrients at a high N:P ratio (Sterner et al. 1992). Most direct measurements of excretion rates of fish and benthic invertebrates reveal relatively low N:P excretion ratios (usually <20 molar; Table 1), as do stoichiometric models for fish (Schindler & Eby 1997, Sterner & George 2000). There is some evidence that unionid mussels have a relatively high N:P excretion ratio (often >20; Nalepa et al. 1991, Davis et al. 2000). However, excretion ratios can be quite variable both among and within species of invertebrates and fish (Nalepa et al. 1991, Arnott & Vanni 1996, Davis et al. 2000, Devine & Vanni 2002, Gido 2002, Vanni et al. 2002). Although Vanni et al. (2002) found that much of the interspecific variation in N:P excretion ratio can be explained by body nutrient ratios and size, clearly more studies are needed that explore interspecific variation in excretion N:P, its relationship to stoichiometry, and its significance for nutrient limitation.

Evidence for the Importance of Nutrient Excretion by Animals: Experimental Studies

HERBIVORES Many studies provide experimental evidence for the importance of herbivores in nutrient cycling. For example, some phytoplankton taxa increase when zooplankton biomass is increased experimentally. These taxa are usually large (hence relatively inedible) and nutrient-limited, suggesting that they are enhanced by nutrient recycling by zooplankton (e.g., Lehman & Sandgren 1985, Elser et al. 1987, Vanni & Temte 1990).

A few investigators have employed a nested design in which herbivory and nutrient cycling processes are experimentally separated. Natural algal assemblages are placed in enclosures with the animals of interest where they are exposed to both grazing and nutrient cycling. In addition, algae are incubated in nutrient-permeable chambers placed inside the enclosures, or sections of the enclosures, that allow passage of nutrients but not animals or algae. Algae incubated in chambers are exposed only to nutrient cycling by animals, and not to direct herbivory. Coker (1983) used this approach and found that nutrient cycling by snails had no effect on algae in an arctic lake. He proposed that nutrient transfer between snails and algae occurs at small scales, e.g., within snail guts or feces. In contrast, Sterner (1986) found that nutrient regeneration by *Daphnia* increased total phytoplankton growth rate as well as that of several taxa; further, the taxon responding most positively to nutrient recycling by *Daphnia* (pennate diatoms) was also the most nutrient-limited.

CARNIVORES AND OMNIVORES Recently, the nested design has been expanded to include effects of higher trophic levels. Vanni & Layne (1997) and Attayde & Hansson (2001a) conducted experiments in lakes. Their enclosures contained fish, zooplankton, and phytoplankton, while nutrient-permeable chambers contained only phytoplankton. Both studies found that some algal taxa responded positively

in nutrient-permeable chambers when fish were present in the surrounding enclosures, showing that these taxa are positively affected by increased nutrient excretion in the presence of fish. Some phytoplankton taxa responded more to nutrient excretion than to direct herbivory, while grazing was more important for others. The extent to which grazing or nutrient cycling has a greater effect on phytoplankton taxa is probably a function of edibility. For example, large (and presumably relatively inedible) taxa such as cyanobacteria and large dinoflagellates are affected much more by nutrient cycling than by grazing (Vanni & Layne 1997, Attayde & Hansson 2001a). However, some relatively edible taxa (e.g., cryptomonads) also responded positively to increased nutrient cycling by animals (Attayde & Hansson 2001a). Geddes (1999) found that algae responded positively to increased nutrient cycling by animals in some nested experiments with a benthic food web containing omnivorous fish and/or shrimp, herbivores, and attached algae.

Thus, in all three of the studies using the nested design with higher trophic levels, increased nutrient availability accounted for some of the observed trophic cascade response, i.e., increased algal biomass stimulated by the top predator. Increased nutrient availability can be mediated by nutrient excretion by top predators themselves (Vanni & Layne 1997), and/or increased nutrient excretion by herbivores (Attayde & Hansson 2001a). Most likely, the relative importance of nutrient excretion by fish and zooplankton will depend on fish biomass, availability of non-planktonic prey for fish, and herbivore size-structure and biomass.

Another experimental approach is to confine fish (the potential source of nutrients) instead of algae (the potential recipients of nutrients) (Schindler 1992, Persson 1997b, Attayde & Hansson 2001b). These experiments have treatments that attempt to isolate the direct effects of fish excretion from other processes, but they differ from the experiments described above in that algae are concurrently exposed to direct herbivory in all treatments. All of these studies showed that phytoplankton abundance and/or productivity was enhanced to some extent by nutrient excretion by fish. However, net effects of excretion by fish on phytoplankton communities may be manifested only when herbivory rates are low (Persson 1997b, Attayde & Hansson 2001b).

TRANSLOCATION EFFECTS OF BENTHIC-FEEDING FISH Havens (1991, 1993), and Schaus & Vanni (2000) experimentally separated nutrient translocation effects from trophic cascade effects of fish on phytoplankton in eutrophic lakes. Some enclosures were fitted with screens placed just above the sediments to prevent fish from feeding on sediments (but allowed them to feed on zooplankton), while in other enclosures fish had access to sediments. Both studies found that when fish had access to sediments, they increased phytoplankton biomass and total P in the water column three- to fivefold and altered phytoplankton community composition (nutrient translocation effect). In contrast, fish had weak or no effects on phytoplankton and water column nutrients when screens prevented them from feeding on sediments (trophic cascade effect). Benthic-feeding fish can also increase water column nutrients and phytoplankton by resuspending sediments (bioturbation, see below), and it is very difficult to separate effects via nutrient excretion

and bioturbation. However, in the experiments described above as well as others with carp (Lamarra 1975), it appears that nutrient translocation (excretion) can account for most of the effects of fish on phytoplankton and nutrients.

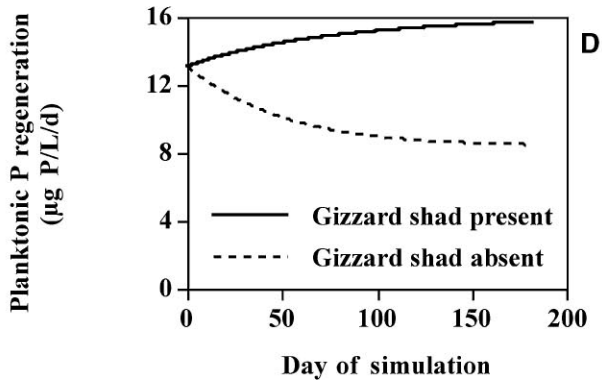
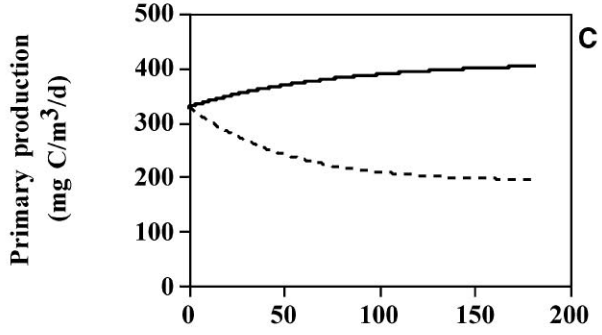
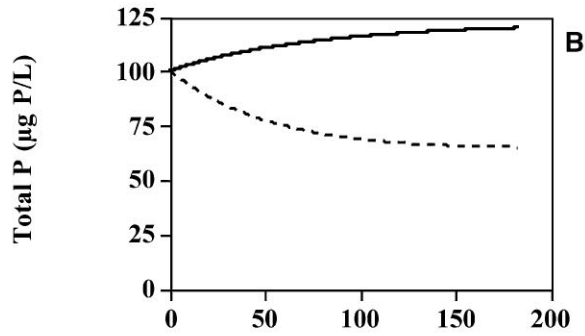
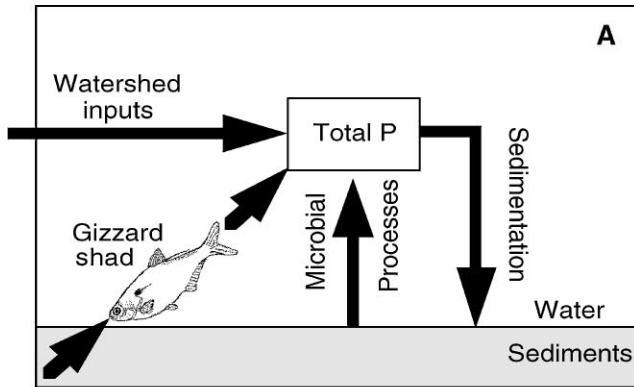
Animals as a Source of New Nutrients: a Simple Model

As mentioned above, some authors have argued that smaller animals such as zooplankton are much more important than fish as nutrient sources (e.g., Hudson et al. 1999.) However, small animals such as zooplankton are more likely to recycle nutrients, whereas large animals like fish often translocate nutrients. Supply of new nutrients may play a critical role in ecosystems (Dugdale & Goering 1967, Caraco et al. 1992). To explore the potential impact of nutrient translocation, here I develop a simple model based on data on nutrient translocation by gizzard shad (*Dorosoma cepedianum*) in Acton Lake, a eutrophic reservoir in Ohio, USA. Gizzard shad is the dominant fish species in this lake (Schaus et al. 1997) and many other lakes in the eastern United States (Stein et al. 1995, Bachmann et al. 1996, Vanni & Headworth in press). In this lake and in most reservoirs, adult gizzard shad obtain most of their energy and nutrients from sediment detritus (Schaus et al. 2002).

In this model (Figure 2), I simulate the dynamics of water column total phosphorus concentration and primary production from May to October, when most production occurs. Gizzard shad excretion rate (P translocation) was set to $0.97 \mu\text{g P L}^{-1} \text{d}^{-1}$, based on data from 1994 to 1999 (Schaus et al. 1997, M.J. Vanni unpublished data). Two other sources of new P were watershed inputs ($1.23 \mu\text{g P L}^{-1} \text{d}^{-1}$, the mean rate of PO_4 inputs from May–October 1994–1998; Vanni et al. 2001), and release of P from sediments ($0.12 \mu\text{g P L}^{-1} \text{d}^{-1}$, based on data from Evarts 1997). Following Smith (1979), primary production in the euphotic zone (PPR, $\text{mg C m}^{-2} \text{d}^{-1}$) was assumed to be a function of water column total phosphorus concentration (TP, $\mu\text{g P L}^{-1}$) based on a relationship for Ohio reservoirs: $\text{PPR} = 8.36\text{TP} - 115.9$ (Knoll et al. 2002). Sedimentation of P was assumed to be the major loss process and was modeled using the relationship between export ratio (ER, proportion of primary production lost via sedimentation) and PPR: $\text{ER} = -0.000163\text{PPR} + 0.459$ (from Table 6 in Baines & Pace 1994). PPR was then multiplied by ER to obtain the loss of C via sedimentation, which was then multiplied by the P:C ratio of sedimenting material (set equal to 0.018 by mass, based on data from sediment traps in Acton Lake) to obtain sedimentation of P from the water column.

Simulations show that nutrient translocation by gizzard shad has major impacts on pelagic P and primary production (Figure 2). With nutrient translocation by gizzard shad, TP and PPR increased gradually, but when translocation was not

Figure 2 Simulation model illustrating effects of nutrient translocation by sediment-feeding fish (gizzard shad, *Dorosoma cepedianum*). *A*: Diagram showing fluxes of phosphorus (P) modeled. *B*, *C*, and *D*: Simulated water column total P, phytoplankton primary production, and planktonic P regeneration with and without nutrient translocation by gizzard shad.



included, TP and PPR declined. Averaged over the simulation period (approximately equal to the length of a growing season), exclusion of gizzard shad excretion resulted in a 35% reduction in TP, which is similar to the effect of shad exclusion in a field experiment (Schaus & Vanni 2000), and a 40% reduction in PPR. Interestingly, this model also showed that regeneration of nutrients by plankton also depends on inputs of new (translocated) nutrients by gizzard shad. I calculated planktonic P regeneration (REG) according to the equation provided by Hudson et al. (1999): $\log \text{REG} = 1.0077 \log \text{TP} + 0.7206$. In the model, planktonic P regeneration declines by 35% when gizzard shad excretion is excluded. In essence, gizzard shad provide new P to the water column that plankton can recycle. Note that even though predicted P excretion by gizzard shad is an order of magnitude less than P excretion by plankton, gizzard shad have major impacts on water column P and primary production because they provide new P. In contrast, because plankton recycle P but do not provide new P, they have no direct impact on water column P concentration.

ANIMALS AS NUTRIENT SINKS

The processes of nutrient consumption and nutrient release by animals may be temporally uncoupled, and this has implications for whether animals function as a nutrient source or sink. Relatively long-lived animals, such as fish and unionid mussels, can sequester large amounts of nutrients in their bodies over timescales relevant to aquatic primary producers. These animals function as a major nutrient sink rather than a source (Kitchell et al. 1979, Kraft 1992, Vaughn & Havenkamp 2001). Kitchell et al. (1975) found that most of the water column phosphorus in highly productive Lake Wingra is stored in fish biomass. Animals are most likely to be important nutrient sinks when their population biomass is expanding and thus sequestering nutrients (Kraft 1992). Zooplankton can also act as nutrient sinks over timescales relevant for phytoplankton. For example, Urabe et al. (1995) found that sequestration of P in *Daphnia* bodies can lead to low rates of P recycling and increased P limitation of phytoplankton.

Nutrients sequestered in animal bodies may be made available as animals die and decompose, thereby liberating nutrients. Kitchell et al. (1979) suggested that remineralization of nutrients from fish bodies following postspawning mortality could be an important P source. Alternating periods of storage and supply through a single population can occur within an ecosystem or among ecosystems. An excellent example of the latter is the migration of Pacific salmon, discussed below.

NUTRIENT TRANSPORT ACROSS ECOSYSTEM BOUNDARIES

In addition to translocating nutrients between habitats within an ecosystem, animals can transport nutrients among ecosystems, often over great distances and long timescales. For example, geese often forage in terrestrial areas and roost in wetlands, transporting nutrients in the process. Geese in the Bosque del Apache

National Wildlife Refuge in New Mexico feed on land but excrete much of their nutrients in wetlands, thereby providing nearly 40% of the N and 75% of the P entering their primary roosting wetland (Post et al. 1998, Kitchell et al. 1999). Stable isotope data also show that these nutrients move up the wetland food web (Kitchell et al. 1999).

Perhaps the most spectacular example of how animals can transport nutrients long distances is that of anadromous Pacific salmon, which can transport nutrients hundreds of kilometers (reviewed by Naiman et al. 2002). Pacific salmon are born and spend their early life in freshwaters, but live most of their life in the ocean where they grow and accumulate the vast majority of their body nutrients. They return to freshwater ecosystems as adults, spawn once, and then die. Remineralization of nutrients from decomposition of adult salmon bodies can represent a major nutrient source to streams and lakes in which salmon spawn (Richey et al. 1975, Kline et al. 1993, Bilby et al. 1996, Finney et al. 2000). Salmon carcasses provide up to 70% of total N inputs (25% on average) into salmon nursery lakes in Alaska (Finney et al. 2000). Because salmon bodies have a relatively low N:P ratio, the contribution of salmon to P inputs is likely to be even greater but is not well quantified (Naiman et al. 2002). Marine-derived nutrients from salmon can also have impacts on riparian terrestrial vegetation, via either direct uptake of nutrients released from carcasses or via urine produced by salmon-eating animals such as bears (Ben-David et al. 1998, Hilderbrand et al. 1999).

Downstream migration of young salmon from freshwaters to the oceans also translocates nutrients, but the quantity of nutrients moved upstream by adult salmon greatly exceeds downstream transport by young fish (Naiman et al. 2002). Thus, anadromous salmon are a sink for marine-derived nutrients, but a nutrient source for freshwaters. Nutrient translocation by salmon historically occurred in thousands of lakes and streams but is being reduced greatly by human-caused declines in salmon populations. This reduction has decreased the productivity of freshwater nursery lakes (Naiman et al. 2002).

INDIRECT EFFECTS OF ANIMALS ON NUTRIENT CYCLING

In addition to effects mediated by the physiological processing of nutrients, animals may have indirect effects on nutrient fluxes. Indirect effects are propagated through direct effects on prey assemblages and/or physical properties of ecosystems. Note that many indirect effects emanate from consumption activities of animals, as do direct effects. However, unlike direct effects, the major pathways for indirect effects are mechanisms other than storage or release of nutrients by the animal initially propagating the effects (Figure 1).

Effects Via Size-Selective Predation

Predation by fish and invertebrates can shift the size distributions of prey assemblages (Brooks & Dodson 1965, Blumenshine et al. 2000). Because mass-specific

nutrient excretion rates of animals decline with body size, size-selective predation can therefore affect nutrient excretion rates of prey assemblages. For example, predation by fish on large zooplankton can shift the zooplankton assemblage to smaller species and therefore increase the rate at which zooplankton recycle nutrients (Bartell & Kitchell 1978, Bartell 1981). Similar effects probably result from size-selective predation on benthic invertebrates or fish. Thus, predators can have important indirect effects on nutrient excretion by animals, even if the predators themselves are not important as direct nutrient sources (Schindler et al. 1993).

Effects on Horizontal Nutrient Transport

EFFECTS ON NUTRIENT UPTAKE LENGTH In running water ecosystems, dissolved nutrients are transported downstream with flow, taken up by organisms on the stream bottom, and then released back into dissolved form for further downstream transport, a process referred to as nutrient spiraling (Webster & Patten 1979). The nutrient uptake length is the length of stream over which a dissolved nutrient molecule travels before being taken up by biota (or abiotic processes) on the stream bottom (Newbold et al. 1981). In general, nutrient uptake lengths are shorter when algae or heterotrophic microbes are nutrient limited and when the biomass of these organisms is high. Animals can affect nutrient uptake length in several ways (Mulholland 1996). Grazing by herbivorous snails increases P uptake length by reducing algal biomass and thus total nutrient demand (Mulholland et al. 1983, 1994; Steinman et al. 1991). Grazers can also alter the relative importance of nutrient sources. For example, when periphyton biomass is high (i.e., when grazing is low), the algal mats represent transient storage zones for nutrients, and most algal nutrient demand is met via recycling within the mat. In contrast, when algal biomass is low, a greater fraction of nutrient demand is met by nutrients flowing by in overlying water (Mulholland et al. 1994). In some ways these two nutrient pools are analogous to recycled and new nutrient categories discussed above for lakes and oceans.

PARTICLE PROCESSING EFFECTS Animals can also affect the size distribution, standing stocks, deposition rates, and transport rates of particles via consumption and egestion, and by "sloppy feeding" (whereby particles are broken up into smaller pieces but not ingested), with subsequent effects on nutrients attached to particles. This is perhaps most important in streams, where many animals ("shredders") feed on large detrital particles (e.g., leaves) and convert them into smaller particles that become available to other consumers such as filter-feeding "collectors" (Cummins & Klug 1979, Webster & Wallace 1996). Via this process, animals can increase the downstream transport of particulate nutrients. For example, experimental removal of macroinvertebrates caused a large reduction in the concentration and downstream transport of fine particulate matter (Wallace et al. 1991). In some tropical streams, sediment-feeding fish can also affect the rate at which sediments (and associated particulate nutrients) accumulate, and thus the

degree to which it is transported downstream (Flecker 1996). Other studies show the impacts of consumption of large particulate organic matter. In tropical Puerto Rico streams, experimental exclusion of shrimp caused decreased leaf decay rates; increased accrual of organic matter, particulate C and particulate N; and increased C:N ratio in material accumulating on the stream bottom (Pringle et al. 1999, March et al. 2001). However, effects depend on the species composition of the shrimp assemblage. By processing leaves into smaller particles one shrimp genus (*Xiphocaris*) increased leaf decay rates, downstream transport of suspended particulate organic matter, and concentrations of dissolved organic carbon and nitrogen (Crowl et al. 2001). Another genus (*Atya*) increased leaf decay rate slightly but had no effect on downstream transport (because they consumed the fine particulates) or dissolved nutrients (Crowl et al. 2001). In contrast to these effects, Rosemond et al. (1998) found that exclusion of fish and shrimp elicited an increase in small invertebrates, but no effects on detrital processing rates in a Costa Rica stream.

BEAVER DAM CONSTRUCTION Dams constructed by beavers (*Castor canadensis*) can greatly affect the downstream transport of nutrients (Naiman et al. 1988, 1994; Correll et al. 2000). In general, the decrease in flow in beaver ponds enhances uptake of dissolved nutrients by algae, sedimentation and retention of particulate nutrients, and denitrification rates (Naiman et al. 1988). Correll et al. (2000) found that a single beaver pond retained or volatilized (i.e., prevented downstream transport of) 18%, 21%, 32%, and 27%, respectively, of total N, P, Si, and suspended solids entering the pond over a six-year period. Over long timescales, nutrients are sequestered in meadows that develop after beaver ponds are abandoned, resulting in long-term reductions in downstream nutrient transport (Naiman et al. 1988, Correll et al. 2000).

Effects on Vertical Fluxes of Nutrients

EFFECTS ON SEDIMENTATION In aquatic ecosystems, particulate matter, including phytoplankton and detritus, can sink from the euphotic zone into the sediments. Sedimentation can represent a major loss of nutrients and productivity from the euphotic zone (e.g., Figure 2; Caraco et al. 1992, Guy et al. 1994), although it may represent a source of nutrients for benthic organisms.

Many studies show that animals can affect the sedimentation of nutrients in lakes, but the effects are quite variable in terms of magnitude, mechanism, and even direction (Uehlinger & Bloesch 1987; Bloesch & Bürgi 1989; Mazumder et al. 1989; Sarnelle 1992, 1999; Elser et al. 1995; Larocque et al. 1996; Houser et al. 2000). Grazing by zooplankton can either increase or decrease nutrient sedimentation rates (Elser et al. 1995, Sarnelle 1999, Houser et al. 2000). Grazing can increase sedimentation rate by shifting size distributions of phytoplankton towards larger phytoplankton taxa, which sink at faster rates than smaller taxa (Mazumder et al. 1989, Larocque et al. 1996) and by production of fecal pellets (Bloesch & Bürgi 1989), which tend to be larger and hence sink faster than phytoplankton.

However, grazing can also decrease net nutrient sedimentation rate by reducing the amount of algal particles, and hence total nutrient mass, in the water column. Thus, nutrient sedimentation rate may decline under high grazing pressure simply because there is less nutrient mass in the water column available for sedimentation (Sarnelle 1992, 1999).

Grazing by zooplankton may increase nutrient sedimentation rate when productivity (nutrient concentration) is high, but decrease sedimentation rate when productivity is low (Houser et al. 2000). However, in some cases sedimentation rate may be maximal at intermediate zooplankton abundance (Sarnelle 1999). The net effects of zooplankton on nutrient sedimentation rate will depend on the direct rate of phytoplankton sinking (a function of phytoplankton size-structure and swimming ability), the proportion of zooplankton fecal material exiting the euphotic zone (a function of zooplankton taxonomic composition, as well as the rate at which fecal nutrients are remineralized, which in turn depends on the depth of the euphotic zone and turbulence), zooplankton assimilation efficiency (which determines fecal production rates), and ecosystem productivity (Elser et al. 1995, Sarnelle 1999).

Some bivalves can also greatly increase the rate at which particles are transported from the water column to the sediments (Strayer et al. 1999, Vaughn & Havenkamp 2001). These benthic organisms filter particles and subsequently deposit some of these (feces as well as particles captured but not consumed) onto the sediments. This can represent a significant loss of energy and nutrients from the water column and shift an ecosystem toward more benthic production and less pelagic production (Strayer et al. 1999).

BIOTURBATION Many aquatic animals, including fish and invertebrates, physically disturb sediments via feeding or other activities, a process known as bioturbation, and this can greatly affect exchange of nutrients between sediments and overlying water. Nutrients often accumulate in sediment porewaters (water in between sediment particles). Physical mixing of sediments by benthic invertebrates can increase the rate at which porewater nutrients are released to overlying waters, and this process can be as important as nutrient excretion by these animals (Gallepp 1979, Graneli 1979, Matisoff et al. 1985, Starkel 1985, Tatrai 1986, Fukuhara & Sakamoto 1987). However, bioturbation can also decrease the rate at which nutrients are released from sediments and therefore can counteract excretion. For example, bioturbation can oxygenate near-surface porewaters by increasing diffusion of oxygen from overlying water. This can lead to increased rates of nitrification of excreted ammonium, increased denitrification rates because of increased nitrate flux to anoxic sediment layers, and/or precipitation of excreted phosphorus (Svensson 1997, Tuominen et al. 1999). The net effects of benthic invertebrates may be taxon-specific. Chironomid excretion products are more likely to be released into the overlying water due to the construction of burrows, which facilitate water movement (Fukuhara & Sakamoto, 1987). In contrast, excretion products of oligochaetes may be trapped in sediments because nutrients are excreted directly into the sediment (Fukuhara & Sakamoto, 1987). Fish can also affect nutrient flux

via bioturbation, either directly by their own activities (e.g., Cline et al. 1994) or by predatory effects on benthic invertebrates (e.g., Svensson et al. 1999).

Atmosphere-Water Fluxes

Effects of animals on nutrient cycling can extend even to fluxes of nutrients between freshwaters and the atmosphere. For example, grazing by stream fishes can increase the abundance of grazing-resistant cyanobacteria, which could result in increased N-fixation rates and thus the total flux of N from the atmosphere (Power et al. 1988). In contrast, MacKay & Elser (1998) showed that nutrient excretion by *Daphnia* in a eutrophic lake reduced the abundance of cyanobacteria and N-fixation rates. Schindler et al. (1997) and Cole et al. (2000) showed that food web structure can affect the flux of CO₂ to the atmosphere. When lakes have relatively low nutrient inputs and food webs dominated by piscivores, then phytoplankton biomass is low, microbial respiration exceeds primary production, lake water is supersaturated with CO₂, and there is a net evacuation of CO₂ to the atmosphere. In contrast, when lakes are dominated by planktivorous fish and have high nutrient inputs, phytoplankton biomass and productivity is higher, and higher algal productivity draws CO₂ into the lake from the atmosphere. These lakes are more likely to be net sinks for CO₂ (Schindler et al. 1997, Cole et al. 2000).

FUTURE DIRECTIONS

It is clear that animals can have strong effects on nutrient cycling in some freshwater ecosystems, but further research is needed to assess generality. Future studies need to take a more holistic approach in terms of nutrient sources, nutrient recipients, and community-level consequences of animal-mediated nutrient cycling. While several studies have compared the importance of nutrient excretion by animals to other nutrient fluxes or to algal nutrient demand, or experimentally explored the role of animal-mediated nutrient cycling, no published studies have included all these approaches. In addition, nutrient demand by heterotrophic microbes as well as algae must be included in supply/demand approaches to achieve an ecosystem scale assessment of the role of animals. While inclusion of all these elements is labor-intensive, it is certainly feasible, and holistic studies will help facilitate the integration of species-based and biogeochemical approaches to ecology (Jones & Lawton 1995).

Future research must determine how often animals play a key role in nutrient cycling and what factors mediate this role. Mediating factors must include characteristics of the animals themselves (e.g., taxonomic affiliation, feeding guild, body size), and the ecosystems in which they reside. With regard to the former, there is considerable interest in ascertaining the roles of species identity and biodiversity in mediating ecosystem processes (Loreau et al. 2001). Exploration of variation among freshwater animals in how they mediate nutrient cycling may offer an excellent means of addressing this question, particularly in tropical ecosystems where

the diversity of species and guilds is very high (Lowe-McConnell 1987, Covich et al. 1999, Vanni et al. 2002). Furthermore, ecological stoichiometry provides a sound theoretical basis for generating predictions about how animals may vary in mediating nutrient cycling (Sterner & Elser 2002, Vanni et al. 2002).

Ecosystem factors probably also affect the importance of animal-mediated nutrient cycling. Ecosystem size is likely to be important. For example, as lake size (surface area) decreases, the ratio of littoral to pelagic habitats increases (Schindler & Scheuerell 2002). Therefore, the role of animals in translocating nutrients from littoral to pelagic habitats is probably greater in small lakes, and most lakes worldwide are small (Wetzel 1990). In contrast, the importance of nutrient recycling within the water column is likely to increase with lake size (Fee et al. 1994). Ecosystem size (e.g., lake surface area, watershed area, stream channel width) may also affect the magnitude of nutrient fluxes from abiotic sources such as watershed runoff, ground water inputs, and wind-mediated nutrient resuspension. The magnitude of these inputs will determine the relative role of animals in supporting the nutrient demands of autotrophs and heterotrophic microbes. Productivity may also be important in mediating the role of animals in nutrient cycling. Attayde & Hansson (2001b) suggested that excretion by animals is more important (relative to herbivory) in unproductive lakes than in productive lakes because nutrient availability is lower in the former. In contrast, Drenner et al. (1998) and Vanni & Headworth (in press) suggest that the importance of nutrient translocation by benthic-feeding fish is likely to increase with lake productivity. No studies have explicitly quantified how nutrient cycling by animals varies with productivity. In addition, factors related to the animals themselves and to ecosystems may interact. For example, species richness and food chain length both increase with lake size, and the former is also related to productivity (Dodson et al. 2000, Post et al. 2001). Species richness and food chain length can mediate the role of animals in nutrient cycling in a number of ways.

Finally, we need to know how the role of animals differs in streams and lakes. Essington & Carpenter (2000) suggested that consumers in streams are most likely to affect nutrient cycling by controlling the rate at which dissolved nutrients are taken up by biota. For example, animals can affect transient storage zones and nutrient uptake lengths via consumption of periphyton mats or detritus. In contrast, Essington & Carpenter (2000) suggest that in lakes, animals are most likely to play a role by converting particulate nutrients into dissolved nutrients via excretion. Certainly, stream ecologists have focused much attention on nutrient uptake length and spiraling (Mulholland 1996, Meyer et al. 1988), and the role of nutrient excretion by animals has been explored much more in lakes than in streams (Table 1). However, it is not clear if the apparently different roles of animals in lakes and streams are real or simply due to different approaches taken by stream and lake ecologists. Webster & Wallace (1996) suggest that the role of nutrient excretion by stream animals warrants much more study, and the few studies that have quantified this in streams demonstrate its importance (Grimm 1988a,b; Hood 2000; Vanni et al. 2002). Future studies need to assess how animal-mediated

nutrient cycling varies between lotic and lentic ecosystems, and along gradients such as ecosystem size, productivity, and species composition.

ACKNOWLEDGMENTS

I thank A.M. Bowling, S.P. Glaholt, S.J. Harper, M.J. Horgan, D.M. Post, A.D. Rosemond, D.E. Schindler, K.A. Sigler, H.M.H. Stevens, and an anonymous reviewer for comments on an earlier draft, and the National Science Foundation (DEB 9615620, 9726877 and 9982124) for supporting my research on nutrient cycling.

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