CHAPTER FIFTEEN

How body size mediates the role of animals in nutrient cycling in aquatic ecosystems

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Introduction

Aquatic ecosystems have been fertile ground for understanding the extent to which animals can alter nutrient cycling. Although animals have been included in ecosystem models for years (for example, Teal, 1962), it is only more recently that investigators have looked at animals, either as individuals, single species, or assemblages, as agents regulating nutrient cycling (Kitchell et al., 1979; Meyer, Schultz & Helfman, 1983; Grimm, 1988; Jones & Lawton, 1995). A recent review details how animals can affect nutrient cycling in freshwater ecosystems (Vanni, 2002), but the next step is to understand the controls on which animals are important regulators of nutrient dynamics in ecosystems. One controlling factor is determined by attributes of the animals themselves, such as their body size.

Animals can regulate nutrient cycling directly or indirectly (Kitchell et al., 1979; Vanni, 2002). Direct regulation is the transformation and transportation of nutrients by animal ingestion, egestion, production and excretion. For example, animal excretion can constitute the largest source of plant-available nitrogen (N) within an ecosystem (Hall, Tank & Dybdahl, 2003) and animals can move nutrients between habitats (Meyer et al., 1983). Perhaps more common are indirect controls, whereby animals alter nutrient cycling by changing the biomass, production or distribution of the plants or microbes that take up nutrients. For example, predatory fish can regulate phosphorus (P) dynamics or nitrogen retention via a trophic cascade (Elser et al., 1998; Simon et al., 2004).

In this paper we consider only direct effects of animals on nutrient cycling, because predicting indirect effects in food webs contains much more uncertainty (Wootton, 1994).

A point mentioned by Vanni (2002), that we expand on here, is the role of body size in controlling the degree to which animals contribute to ecosystem nutrient fluxes. Body size may control animal-mediated nutrient cycling by three main mechanisms. First, small animals have higher metabolism and, therefore, higher mass-specific excretion rates (Wen & Peters, 1994; Brown, Allen & Gillooly, this volume). Thus, total biomass being equal, an assemblage with small animals may have higher animal-mediated nutrient fluxes than one with large animals. Second, as body size increases, allometric variation in structural tissue (e.g. P-rich bone) may alter ratios of excreted nutrients. Third, large animals have larger home ranges and are more likely to migrate long distances, so nutrient translocation by animals may also be a function of body size.

In this chapter we first address how body size controls nutrient fluxes in the context of the first two mechanisms described above by using published and unpublished data to examine the relationship between nutrient excretion and body size. We also consider the spatial and temporal translocation of nutrients by animal movements as a function of body size. In the second part of the chapter we apply these findings to address how ecosystem-level nutrient cycling will change as a function of variation in animal body size. In short, we know excretion can vary as a function of body size, but does this variation matter in ecosystems? We explore other factors that affect animal-mediated nutrient cycling, such as variation in the biomass of animal assemblages and their taxonomic composition, so that we can compare their influence to the effects of body size. Lastly, predators, especially humans, may alter the size structure of animal assemblages, and we consider how loss of large-bodied organism may indirectly alter nutrient cycling (see also Jennings & Reynolds, this volume).

**Body size and nutrient excretion**

**Rates**

Aquatic animals excrete N and P in mostly mineral forms which are readily taken up by microbes. The primary form of N is ammonium, which is excreted via the gut in insects, or diffuses across the integument and gills of other animals. Animals primarily excrete P in the form of $PO_4^{3-}$. Nutrient excretion rates vary with body size. In general, excretion rates ($E$) scale allometrically with body mass ($M$):

$$E = aM^b$$

(15.1)

where $a$ and $b$ are constants (Huxley, 1932; Peters, 1983; Wen & Peters, 1994; Gillooly *et al.*, 2001). For most aquatic animals, the relationship has an exponent $b < 1$ indicating that excretion rates increase at a rate less than isometric with
increasing body size (Wen & Peters, 1994). For example, individual ammonium excretion rates for stream invertebrates, from at least 18 taxonomic orders, scale to the 0.85 power of body mass (Fig. 15.1), implying that larger taxa excrete at a lower rate for their size than smaller taxa. The mechanism for the less than proportional increase in excretion rate is probably linked to metabolism, which scales as the 3/4 power of body size (Brown et al., 2004; Brown et al., this volume). However, for many specific groups of animals, $b$ can be higher or lower than 3/4. For example, $b = 0.67$ for N and 0.54 for P in zooplankton (Wen & Peters, 1994), whereas macroinvertebrates (Fig. 15.1) are higher.

However, body size is not the sole factor controlling variation in animal excretion rate. It is worth considering the influence of other variables, that may alter or interact with the effects of body size, on animal-mediated nutrient cycling in aquatic ecosystems. For example, temperature influences metabolic processes, such as excretion rate (Peters, 1983; Fukuhara & Yasuda, 1989; Zhuang, 2005) Metabolic theory (Gillooly et al., 2001; Brown et al., 2004; Brown et al., this volume) provides a mechanistic framework for incorporating the effects of both temperature and body size on excretion rate. Fed animals have higher excretion rates than unfed animals (Gardner & Scavia, 1981; Grimm,

![Figure 15.1](image_url)

**Figure 15.1** Ammonium excretion rates increase less than proportionally with body size ($b < 1$) for many benthic stream invertebrate taxa, indicating that larger invertebrates excrete ammonium at a lower rate per mg of body mass than do smaller invertebrates. The regression line ($\log_{10}\text{excretion rate} = -1.057 + 0.853\log_{10}\text{mean individual body mass}$; $n = 320$, $r^2 = 0.381$, 95% CI on $b$ [0.776 – 0.937]) was estimated using type II, reduced major axis linear regression (Bohonak & van der Linde, 2004). Data points were gathered using identical methods on field-caught animals from six streams and represent total excretion rates computed from one or more similarly-sized individuals of the same taxon within the same incubated container (Hall et al., 2003; R. O. Hall, unpublished data; Koch, 2005; M. C. Marshall, unpublished data).
1988), probably because of active metabolism of recently digested and assimilated N compounds. The use of fed or unfed animals may have contributed to the variability in Fig. 15.1 and make studies where methods differ less comparable.

Taxonomic differences can also explain some of the variation in invertebrate nutrient excretion rates (Wen & Peters, 1994). For example, Conroy et al. (2005) found taxonomic differences in excretion rates of P, but not of N, between two species of mussels in the genus *Dreissena*. Interestingly, in contrast to nearly all other freshwater invertebrate taxa studied to date, N and P excretion rates for *Dreissena* increase disproportionately with body size ($b = 1.379$), such that larger individuals excrete nutrients at a higher mass-specific rate than do smaller individuals (Conroy et al., 2005). The mechanisms behind this relationship are unclear, although it highlights the importance of recognizing taxonomy in studies of animal-mediated nutrient cycling.

To examine taxonomic and size variation in excretion rates among fishes, we compared published fish excretion rates of individuals ($n = 156$ for P and 163 for N) and species means ($n = 30$ species for P and N) among freshwater representatives of 14 families, including Anostomidae, Aspredinidae, Catostomidae, Cetopsidae, Characidae, Characidiidae, Cichlidae, Clupeidae, Curimatidae, Loricariidae, Parodontidae, Pimelodidae, Salmonidae and Trichomycteridae (Schaus et al., 1997b; Gido, 2002; Vanni et al., 2002; Andre, Hecky & Duthie, 2003; B. J. Koch, unpublished data). Individual rates are the excretion of a single fish (many individuals in a species were measured) and species means were calculated by averaging the excretion and size of all the individuals in that species. All studies measured ammonium, but Schaus et al. (1997a) and Andre et al. (2003) measured soluble reactive P, Vanni et al. (2002) estimated total dissolved P, while Gido (2002) measured total reactive P. We converted wet mass to dry mass by assuming dry mass was 25% of wet mass (Schaus et al., 1997a; Gido, 2002; Andre et al., 2003), or used measured values directly (Vanni et al., 2002; B. J. Koch, unpublished data).

Excretion of individuals within a species scaled with body size similarly, and were higher or lower than the species means (Table 15.1). The P excretion of three species scaled less than 1 (Table 15.1; Fig. 15.2a), meaning that the mass-specific excretion rates declined with increasing size. However, N excretion of species showed greater variability ($b < 1$, $b = 1$, $b > 1$), indicating that both size and taxonomy influence rates (Table 15.1; Fig. 15.2b). When fish species means were considered, excretion scaled proportionally with dry mass (that is $b \sim 1$; Table 15.1, Figs. 15.2c,d). These data cannot disentangle the relative contribution of phylogeny vs. size because they are not independent. However, comparing species means to individual species, we can conclude that fish scale similarly to each other. Additionally, measurements were collected by different researchers under different conditions, which may cause high variation in excretion rates among all fishes.
The relative importance of taxonomy, body size and temperature in controlling nutrient excretion rates is only just beginning to be explored, and adequately testing the interactions among these factors will require richer datasets and resolved molecular phylogenies. In addition, determining the basis of taxonomic variation in excretion rates remains a challenge. Body nutrient composition and diet may both play roles. Given that ammonium excretion rates for stream invertebrates are higher for fed than unfed animals (Grimm, 1988), predators, which feed sporadically, may have more variable excretion rates over time than continuously feeding grazers and detritivores. Stoichiometric differences in animal nutrient use might also drive taxonomic variation (Elser & Urabe, 1999). Predators, with relatively N-rich diets, may have higher N excretion rates than other feeding groups. Understanding when to account for taxonomic variation and when body size alone is sufficient for studies of animal-mediated nutrient cycling is central to predict successfully the role of animals in the nutrient dynamics of aquatic ecosystems.

Table 15.1 Reduced major axis regression estimates for nitrogen and phosphorus excretion \((\log_{10} \mu g N \text{ or } P \text{ fish}^{-1} \text{ h}^{-1})\) and size \((\log_{10} \text{ dry mass, g})\) in five groups of fish (see Fig. 15.2). Data for Mbuna Cichlidae, Carpiodes carpio, Ictiobus bubalus and Dorosoma cepedianum estimates are excretion rates from individual fish within a taxon. We also calculated the mean excretion rate and size of 30 fish species taken from Gido (2002); Vanni et al. (2002); Andre et al. (2003); Schaus et al. (1997b); and Koch (unpublished data) and regressed mean excretion rate on mean body size. The bootstrapped 95% confidence intervals of the exponents are in parentheses.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Nitrogen</th>
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<th>Phosphorus</th>
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<tr>
<td></td>
<td>n</td>
<td>Intercept</td>
<td>Exponent</td>
<td>(r^2)</td>
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<tr>
<td>Mbuna* Cichlidae</td>
<td>40</td>
<td>2.04</td>
<td>0.759 (0.664–0.886)</td>
<td>0.769</td>
</tr>
<tr>
<td>Carpiodes carpio</td>
<td>10</td>
<td>2.96</td>
<td>0.789 (0.525–1.06)</td>
<td>0.770</td>
</tr>
<tr>
<td>Ictiobus bubalus</td>
<td>16</td>
<td>2.27</td>
<td>0.983 (0.764–1.43)</td>
<td>0.633</td>
</tr>
<tr>
<td>Dorosoma cepedianum</td>
<td>93</td>
<td>2.13</td>
<td>1.14 (1.04–1.24)</td>
<td>0.883</td>
</tr>
<tr>
<td>Species means</td>
<td>30</td>
<td>2.41</td>
<td>0.953 (0.851–1.05)</td>
<td>0.930</td>
</tr>
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\(^{1}\) Gido (2002)
\(^{2}\) Vanni et al. (2002)
\(^{3}\) Andre et al. (2003)
\(^{4}\) Schaus et al. (1997b)
Ratios of N and P

Not only will the amount of N and P excreted by animals be important in ecosystem nutrient cycling, but the ratio of these nutrients may also drive microbial assemblage structure and productivity (Elser et al., 1988). Nutrient ratios in food sources, animal composition and excretion (that is, ecological stoichiometry) have received much attention in aquatic ecology (Sterner & Elser, 2002). Stoichiometric theory predicts that the N:P in excretion is a positive function of the N:P of ingested food, and a negative function of the N:P requirement of the consumer (Sterner, 1990). Data show that the link between N:P in the zooplankton body and excreted N:P is not nearly as strong as the link with the N:P of their food (Elser & Urabe, 1999); that is, most of the variance in excreted N:P is accounted for by variation in the food. Few analyses show how body size drives the N:P in excretion in animals; indeed, there is little information on animal C:N:P content solely as a function of body size (Sterner & Elser, 2002). One hypothesis might be that aquatic animals should increase their N:P content as size increases, because increased size should lead to decreased demand for P as growth rate declines (Elser et al., 1996). Given higher body N:P, big animals should have lower excreted N:P than small ones. However,
this effect may be hidden by phylogeny and allometric constraints, as taxonomy correlates with body size because large animals are often vertebrates that have high P storage in bone apatite, and presumably a high N:P in excreta.

Data on aquatic animals suggest that excreted N:P increases with body size. Wen and Peters (1994), showed that log N excretion rate (μg N/d) increased more steeply with body mass than did excreted P for zooplankton. The difference in the exponents is 0.13, which corresponds to the exponent for N:P of excretion vs. body mass. Thus the N:P of excretion increases with body mass, suggesting that mechanisms other than growth rate control the relationship of excreted N:P with body size.

Data from some vertebrates also suggest increases in the N:P excreted with body size. Excretion N:P in fishes and amphibians from a Piedmont stream in Venezuela was positively related to body size, which agrees with qualitative predictions based on a decreasing body N:P with increasing body mass in vertebrates (Vanni et al., 2002b). For example, bony-scaled armoured catfishes (Loricariidae) had particularly low body N:P and therefore high N:P in excretion (Vanni et al., 2002). Tadpoles (families Bufonidae and Ranidae) had low excreted N:P; because they do not have ossified bones (low skeletal demand for P). These studies, although few, suggest that not only will body size determine the rates of nutrient regeneration, but it will also determine the ratio of these nutrients, with the data so far suggesting mostly increasing N:P with body size. Mechanisms for this increase are unclear, and certainly vary across taxa. For example, vertebrates will have proportionally more bone as their size increases (Sterner & Elser, 2002), which will increase P demand (lowering P excretion) with body size.

**Body size and nutrient translocation**

Aquatic animals can alter nutrient cycling by moving nutrients from one location to another, thus subsidizing the receiving habitat (Kitchell et al., 1979; Vanni, 2002). In some instances this nutrient movement is between habitats within an ecosystem such as, for example, benthic feeding fish that excrete nutrients in the pelagic zone (Vadeboncoeur, Vander Zanden & Lodge, 2002) or haemulid grunts that feed in seagrass beds at night and rest above coral heads during the day, where they release nutrients that stimulate coral growth (Meyer et al., 1983). In other cases, animals move nutrients between ecosystems on a daily basis; e.g. ocean-foraging river otters (Lontra canadensis) excrete nutrients in discrete locations in terrestrial habitat (Ben-David et al., 2005). Less mobile or small-sized animals may actually concentrate nutrients at high levels in localized areas (Reinertsen et al., 1986). In contrast, Pacific salmon (Onchorhynchus spp.) transport nutrients from the ocean to rivers via an annual long-distance spawning migration (Gende et al., 2002). The degree of movement will be determined in part by the speed at which animals move and the behavioural...
constraints on their home range. Both of these controls on movements should scale with body size.

The distance moved by aquatic animals will depend on their body size because swimming speed scales with animal body size (Peters, 1983). For a given time travelled, a big animal can migrate further than a small one. Over large size ranges, an animal’s Reynolds number constrains movement (e.g., zooplankter versus a salmon). Small animals (e.g., rotifers) move very slowly because their short length confers a low Reynolds number, and therefore viscous forces are much higher than inertial forces. Within fishes that have high Reynolds numbers, swimming speed scales at about $M^{0.14}$ (Weihs, 1977) assuming $M \propto L^{2.6}$ (Peters, 1983). These modelled swimming speeds include both Reynolds number effects plus allometric scaling of swimming force and metabolic costs. Animals with lower Reynolds numbers have a steeper positive relationship between body mass and swimming speed, probably because of the more pronounced effects of viscous forces at small sizes. Swimming speed in diving beetles (Dytiscidae), increases as $M^{0.36}$ (Nachtigall, 1977) assuming $M \propto L^{2.5}$ (Benke et al., 1999). Thus, the decline in swimming speed for small animals probably decreases more quickly with body size than it does for fish.

Behavioural constraints on home-range size and migration will also control nutrient movement by animals. Home range scales with body size in mammals at roughly $M^1$ (Jetz et al., 2004). Home-range sizes of fishes are similar to mammals, scaling as $M^{1.1}$, while insects and crustaceans are at $M^{0.7}$ and molluscs at $M^{0.55}$ (Alimov, 2003). Given that distance moved will scale as the square-root of area, distance moved for fishes should then scale as approximately $M^{0.5}$. This rate of increase with body size in the actual distance moved by animals is higher than that for speed alone, because home range is determined by many more attributes than is speed. These include, for example, resource requirements and interactions with conspecifics (Jetz et al., 2004). Animals that transport substantial nutrients among habitats are likely to be large, as in Pacific salmon (Gende et al., 2002), river otters, (Ben-David et al., 2005), and the long-distance migratory fish, sapuara (Semaprochilodus kneri) (Winemiller & Jepsen, 2004). It is important to consider the strong effect of behaviour; the much smaller sapuara migrates long distances along rivers, and therefore transfers nutrients much further than does the coastal river otter. Coral reef fishes are large enough to travel long distances, but many stay in one spot on the reef all their lives. Thus, while large animals are more likely to move nutrients, behavioural characteristics also control this distance.

Consequences of size-varying nutrient cycling

Variation in body-size distributions

Because excretion rates typically increase less than proportionally with animal body size, variation in size distributions can partially control animal-driven
nutrient mineralization and storage in ecosystems. Here we ask to what degree does variation in animal size distribution regulate nutrient mineralization? Researchers have described a wide variety of biomass-size distributions (also called size spectra) for aquatic animal assemblages, including flat or smooth, uni-, bi- and poly-modal, and step or asymptotic functions. Size distributions can vary considerably in space and time within and among aquatic habitats (Hanson, Prepas & Mackay, 1989; Stead et al., 2005), complicating generalizations (see Warwick, this volume). The diversity of methods in body-size estimations (for example, Morin & Nadon, 1991; Ramsay et al., 1997; Baca & Threlkeld, 2000) and analytical techniques, such as different sieve or size classes, further complicate size-spectra summaries (Cyr & Pace, 1993; Robson, Barmuta & Fairweather, 2005). However, when only the invertebrate portions of published aquatic assemblage spectra are included (that is, smaller and larger portions excluded), clearer patterns of shape categories emerge. Most size spectra have biomass peaks that are skewed left, meaning larger animals generally account for most of the total biomass, even though they may be outnumbered by smaller ones.

Size distributions in lakes vary as a function of habitat. Studies that include multiple habitat types within the same lake suggest that pelagic and littoral assemblages tend to have bimodal distributions of invertebrates (Hanson et al., 1989; Cyr & Pace, 1993; Rasmussen, 1993) and polymodal distributions when fishes are included (Gaedke, 1992), whereas profundal (and sublittoral) distributions tend to be unimodal (Hanson et al., 1989). The magnitude and locations of biomass peaks and troughs also vary among habitats within lakes; littoral habitats have peaks at larger body sizes. For example, the two biomass maxima for littoral habitats tended to occur between 1–4 mg and 64–256 mg wet mass (Rasmussen, 1993), whereas the two peak densities of pelagic zooplankton occurred between 0.044–0.125 µg and 2.0–11.3 µg dry mass for small and large animals, respectively (Cyr & Pace, 1993).

Streams generally have unimodal biomass size distributions (Cattaneo, 1993; Bourassa & Morin, 1995; Mercier et al., 1999; Schmid, Tokeshi & Schmid-Araya, 2002). Body-size maxima, as equivalent to a spherical diameter, were between 2–4 mm in streams (Cattaneo, 1993), and the average individual biomass increased slightly with increasing trophic status from 24–40 µg dry mass in oligotrophic to urban eutrophic streams, respectively (Bourassa & Morin, 1995). Overall, although unimodality is robust across many streams, total biomass can vary by an order of magnitude (for example, Bourassa & Morin, 1995) suggesting possible dramatic differences in animal driven nutrient fluxes within a stream system.

**Estimating nutrient flux from biomass size distributions**

Animal assemblages with different size distributions should have different nutrient supply rates to ecosystems, all else being equal. To illustrate this
point we used data-capturing software to extract published size spectra from plots. We gathered three representative aquatic animal size spectra: a bimodal distribution with proportionally more large individuals (Fig. 15.3a), a strongly peaked bimodal distribution (Fig. 15.3b) and a unimodal distribution (Fig. 15.3c, Rasmussen, 1993). We assumed dry mass was 25% of wet mass (Feller & Warwick, 1988) and normalized the literature spectra data to have equivalent total biomasses (1000 mg dry mass m$^{-2}$) while preserving the same distribution shape in the original data sets. For each of these three animal assemblages, we then calculated the P flux supplied by excretion for each size class (Figs. 15.3d-f), using a negative relationship between mass-specific excretion rate and body size ($\mu$g P mg dry mass$^{-1}$ h$^{-1}$ = 0.0954[dry mass]$^{0.54-1}$, Wen & Peters, 1994). While this analysis accounts for variation in animal excretion rate due to body size, it does not incorporate the effects of potentially different temperatures or taxonomic composition among animal assemblages. Nevertheless, despite total biomass being the same for the three communities, total nutrient flux (cumulative area of rectangles) from each of the three animal communities is not equivalent, varying by almost a factor of two in this example (60, 115 and 104 $\mu$g P m$^{-2}$ h$^{-1}$ for Figs. 15.3d,e & f, respectively). Furthermore, the shapes of the

Figure 15.3 (a–c) Representative animal size spectra from three littoral ecosystems: (a) Lake Brome, (b) Lake Waterloo, (c) Lake Bromont (Rasmussen, 1993). Total biomass (mg dry mass m$^{-2}$) has been normalized to 1000 mg dry mass m$^{-2}$ for the three communities. Size classes are $\text{Log}_2$ (mg dry mass). (d–f) Modelled P fluxes ($\mu$g P m$^{-2}$ h$^{-1}$) supplied by excretion for the three assemblages, assuming a negative relationship between mass-specific excretion rate and body size. Total nutrient flux varies nearly two-fold for the three communities (60, 115 and 104 $\mu$g P m$^{-2}$ h$^{-1}$ for panels d, e and f, respectively) and the shapes of nutrient flux distributions changed relative to size spectra.
nutrient flux distributions differ from their respective biomass size spectra. For example, although larger animals comprise most of the total biomass in Fig. 15.3a, small- and medium-sized animals supply the bulk of the nutrient flux from this assemblage (Fig. 15.3d). Thus the size spectra of animal communities have important consequences on the supply and cycling of nutrients, and those size classes that contribute most to total assemblage nutrient flux are not necessarily the most biomass-rich size classes in the assemblage.

Predator control of prey body size and nutrient cycling

The well-known impact of predators on prey size structure may alter nutrient cycling in aquatic ecosystems. Fish predators can decrease average size of prey by eating large zooplankton (for example, Brooks & Dodson, 1965; Li, Wetterer & Hairston, 1985) and large benthic invertebrates in lakes (Blumenshine, Lodge & Hodgson, 2000). Alternatively, planktonic invertebrate predators, such as *Chaoborus*, select small zooplankton (for example, Dodson, 1974), increasing average prey body size. In streams, predatory invertebrates, fish and mammals tend to consume the largest individuals of their prey (Quinn & Kinnison, 1999; Allan, 2001; Woodward & Warren, this volume).

In addition to changes in size structure via consumptive effects, the presence of predators can alter prey-size distribution simply through non-consumptive effects, such as chemical cues (for example, Tollrian, 1995; Peckarsky *et al.*, 2002) and excretion (Ramcharan, France & McQueen, 1996). Simultaneous to their effects on body size, predators can also affect prey physiology by increasing the allocation of nutrients to structural cells, (for example, Lively, 1986; Vanni, 1987; Crowl & Covich, 1990; Stibor, 1992; Barry, 1994; Arendt & Wilson, 2000; Dahl & Peckarsky, 2002), which may change the composition of consumer-mineralized nutrients.

Altered size structure of the prey assemblage may change nutrient cycling, because mass-specific excretion rate decreases with increasing animal size. Additionally, body size affects the nutrient ratios at which animals excrete. Changes in excretion N:P can alter the supply of the nutrient that limits primary producers. Elser *et al.* (1988) suggest that phytoplankton communities are more likely P-limited when the zooplankton assemblage includes large-bodied individuals and N-limited when the zooplankton assemblage is mainly small-bodied individuals.

Understanding how changes in the size structure of prey can affect nutrient cycling is not straightforward, because predators can simultaneously alter prey abundance and biomass, and regenerate nutrients by consuming prey. Bartell (1981) modelled P cycling under differing levels of predation using previously published data on zooplankton size and biomass in lakes, and a mass-specific excretion model for zooplankton. Nutrient fluxes from zooplankton did not always increase when the assemblage switched from large-bodied to the
small-bodied individuals that have greater mass-specific excretion rates. In fact, P fluxes either remained similar, increased or decreased when lakes were altered from low to high planktivore abundance, depending on changes in total zooplankton biomass. However, nutrients may be more available in lakes with abundant zooplanktivorous fish, because smaller zooplankton turn P over faster than larger-bodied zooplankton (Henry, 1985). In addition to zooplankton, fish can also be an important source of nutrients to primary producers. Some studies have reported that the nutrient flux from zooplankton is much larger than fluxes from fish (Ramcharan et al., 1996), while others found the reverse (Vanni & Findlay, 1990; Carpenter et al., 1992). Boers, Vanballeghooijen & Uunk, (1991) showed that the main P source switched from zooplankton to fish as planktivore biomass increased.

Regardless of which animal supplies more nutrients, their body size can affect nutrient cycling. To illustrate how size structure can change nutrient supply and demand we use lakes with low and high planktivorous fish abundance. In lakes with low planktivore abundance, both large and small zooplankton may be present (Fig. 15.4a), but the assemblage is mainly composed of small zooplankton when planktivores are abundant (solid line, Fig. 15.4c). Compensatory increases in the number of small zooplankton may result when fish are present (dashed line, Fig. 15.4c); however, most studies show an overall decrease in total zooplankton biomass (for example, Vanni & Findlay, 1990). When the density of planktivorous fish is low (that is, both large and small zooplankton are present), zooplankton excrete at a range of N:P ratios (grey line is N; black line is P; Figure 15.4b); however, zooplankton excrete at a lower N:P ratio when planktivorous fish are abundant (causing N to be potentially limiting). Based on modelling by Bartell (1981), changes in zooplankton size structure may either increase, decrease or not change lake nutrient fluxes (Fig. 15.4d), depending on compensatory changes in assemblage biomass. In contrast to planktivorous fish, planktonic-invertebrate predators selectively consume small zooplankton, resulting in a large-bodied prey assemblage excreting at a high N:P ratio. Depending on biomass, prey nutrient fluxes could change in either direction but may cause P to be limiting.

The effect of predators on zooplankton body size in temperate lakes is well known; however, to our knowledge no studies have investigated how shifts in body size of stream invertebrates could alter nutrient cycling. Because stream predators selectively consume large-bodied prey, similar to planktivores feeding on zooplankton, we suggest that a decline in N:P mineralization and an increase in mineralization rates may hold for streams. However, even with the advances in methods to estimate pools and fluxes of nutrients in streams, the effects of predators on prey body size and nutrient cycling has not been investigated, even though in certain cases stream invertebrates can be an important source of ammonium (Grimm, 1988; Hall et al., 2003; Koch, 2005).
The effect of harvesting-induced changes in animal size structure on nutrient cycling

Harvesting by humans affects the size structure of aquatic animal assemblages, and these altered size distributions may affect the rates and types of nutrients mineralized by animals (Jennings & Reynolds, this volume; Persson & De Roos, this volume). Similar to many other animals, humans selectively harvest large individuals and species (Pauly et al., 1998; Jackson et al., 2001; Roy et al., 2003; Allan et al., 2005). Size-selective harvesting can substantially change species composition and food-web structure (for example, removal of predators), leading to fishing down the food web—a process by which larger species, often predators, with slower growth rates are successively removed from the assemblage, leaving smaller species with faster growth rates (and thus higher mass-specific nutrient excretion) that occupy lower trophic levels (Pauly et al., 1998; Welcomme, 1999). In addition, size-selective harvesting can decrease body size indirectly, by causing earlier maturation at smaller sizes via rapid evolutionary
change or increased resource availability that accelerates growth and decreases time to maturity of the remaining individuals (Trippel, 1995). Taken together, human harvesting generally decreases or eliminates the biomass of large animals from an ecosystem (Myers & Worm, 2003; Allan et al., 2005; Ward & Myers, 2005).

There are several mechanisms by which harvest-induced changes in animal body size may alter the role of aquatic animals in mineralizing nutrients. Foremost, size-selective harvesting results in the loss of large-bodied individuals and species with high excretion rates per individual, but low mass-specific excretion. There are also important differences in the ratios at which limiting nutrients, such as N and P, are released by animals of different size (Wen & Peters, 1994; Schindler & Eby, 1997; Sterner & Elser, 2002; Vanni et al., 2002). As a result, the removal of large individuals may disproportionately reduce the amount of N relative to P supplied by animal assemblages (Fig. 15.4a,b), assuming there is no compensatory increase in abundances of smaller individuals or species (solid line; Fig. 15.4c). If there are compensatory increases in abundance of smaller individuals or species (dashed line; Fig. 15.4c) with higher mass-specific mineralization rates, then the total supply of nutrients by the assemblage experiencing harvesting may equal or surpass the amount supplied by the assemblage before harvesting (Fig. 15.4d). In addition, because home-range size and migration distance increases with body size (Brown, 1995; Alimov, 2003; Jetz et al., 2004), reduced body size due to harvesting could also decrease the spatial scale over which nutrients are distributed by animals. This impact has been realized; harvesting of large, migratory salmon may have decreased marine nutrient loads to inland rivers, potentially lowering their productivity (Thomas et al., 2003). Moreover, the larger animals, which are often the first and most intensely harvested, generally have longer lifespans and more stable population cycles than the smaller, short-lived species that are less frequently harvested. Therefore, the removal of large, long-lived animals could increase the fluctuations of nutrients mineralized by animal populations.

Overharvesting of large animals is a hallmark of all aquatic environments (Myers & Worm, 2003; Allan et al., 2005). However, surprisingly little is known about how the removal of larger animals alters the type or supply rate of nutrients mineralized by animal assemblages and, more importantly, whether such changes in nutrients are large enough to alter ecosystem-level processes. In the Baltic sea, Hjerne and Hansson (2002) estimated that the removal of N and P in fish biomass by harvesting to be 1.4–7% of the total nutrient load, although the nutrient loss due to decreased mineralization by fish was not quantified. Although information is available on how predators can mediate nutrient mineralization rates by altering the size-structure of their prey, the process and long-term effects of harvesting by humans are likely to be very different. Humans typically remove the biomass of the largest animals, rarely switch
prey until populations are severely reduced or regulatory restrictions are imposed, and harvest at maximal rates, which are often supported by external factors such as economic subsidies. In freshwater, species removals for biomani-  

pulation (Horppila, 1998; Tarvainen, Sarvala & Helminen, 2002), and declines in introduced species, affect nutrient fluxes (Kraft, 1993); however, few studies have documented the direct effects of size-selective harvesting on nutrient fluxes. One reason is the mismatch in the data that are available on nutrient mineralization rates and harvesting rates of aquatic animals between marine and freshwater ecosystems. There are comparatively better data on catch size and body size of marine animals (Pauly et al., 1998; Myers & Worm, 2003; Ward & Myers, 2005) than freshwater animals (Allan et al., 2005), whereas there are more empirical data on nutrient regeneration rates for freshwater animals (Sterner & Elser, 2002). In marine systems, it may be useful to apply bioenergetic models to estimate the amount and type of nutrients lost from these systems as a result of having removed 80% of the large predatory fish biomass (Myers & Worm, 2003). Predicting the effects of harvesting-induced changes in body size on nutrient cycling is a new challenge that could improve our understanding of the role of animals in ecosystem functioning, and provide urgently needed guidance for managing and restoring these systems.

The next steps?

Given that animals can often be important regenerators, storers and transporters of nutrients in ecosystems (Kitchell et al., 1979; Gende et al., 2002; Vanni, 2002; Koch, 2005), body size may be the single most important trait of the animals themselves in controlling these processes. There are plenty of avenues in which to further explore the role of body size in conjunction with other animal attributes (for example, phylogeny), and ecosystem processes. Below we give some of these examples.

1. Taxonomic identity probably determines a large fraction of variation in excretion rates, and taxonomy covaries with body size. To what degree does size alone determine nutrient excretion rates? Can we integrate size and phylogeny to improve predictions of nutrient excretion rate?
2. Body size allows us to examine how traits of animals impact ecosystem processes, but we cannot forget that the attributes of the ecosystems themselves will, in part, determine the impact. For example, plant nutrient demand, disturbance and hydrologic flushing rates are certainly important. How important is animal assemblage structure relative to physical controls and plant/microbial demand for nutrients?
3. We can only speculate as to the potential role of many fisheries on changes to nutrient cycling. Some are well known, (for example, salmon), but most are unknown (for example, groundfish stocks). These human-induced
changes present an opportunity to examine how changes in aquatic animal assemblages affect ecosystem processes and may provide the means to compare the relative importance of direct versus indirect effects of assemblage and size structure on nutrient cycling.

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