

Organism Size, Life History, and N:P Stoichiometry

Toward a unified view of cellular and ecosystem processes

James J. Elser, Dean R. Dobberfuhl, Neil A. MacKay, and John H. Schampel

Ecosystem science and evolutionary biology have long been infrequent and uncomfortable bedfellows (Hagen 1992, Holt 1995, McIntosh 1985). However, the convergence of a global decline in biodiversity and global alterations in biogeochemical cycles provides motivation to overcome past inhibitions. Currently, attempts are being made (Jones and Lawton 1995) to understand relationships between the foci of evolutionary biology (the individual in its species population) and ecosystem science (energy and material flow and storage). Analysis of relationships between species and ecosystems requires a framework appropriate for moving between levels

James J. Elser is an associate professor in the Department of Zoology, Arizona State University, Tempe, AZ 85287. His research interests include trophic interactions and nutrient cycling in ecosystems. Dean R. Dobberfuhl is a doctoral candidate whose research interests include phylogenetic and evolutionary determinants of biochemical and elemental content of invertebrates. Neil A. MacKay is a doctoral candidate whose research interests include behavioral ecology of zooplankton and zooplankton-cyanobacteria interactions. John H. Schampel is an assistant research scientist whose research interests include zooplankton-phytoplankton interactions, zooplankton physiological ecology, and applied limnology. His present address is Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108. © 1996 American Institute of Biological Sciences.

**Elemental
stoichiometry can
provide a new tool to
trace the threads of
causal mechanisms
linking cellular,
ecosystem, and
evolutionary processes**

in an imperfect hierarchy of biotic and abiotic components (O'Neill et al. 1986). Although various frameworks are possible, the history of ecology since Lindeman's 1942 paper on the trophic dynamic concept makes it clear that energy has been the currency of choice for ecologists (Hagen 1992).

Although the energetics perspective has had wide application and success, both in studies of individuals and of ecosystems (Brown 1995, Pandian and Vernberg 1987, Wiegert 1988, Wright et al. 1994), critical examination reveals inadequacies in this paradigm. For example, White (1993) argues that, because of disparities between the nitrogen composition of many foods and the nitrogen demands of many consumers, the availability of energy is less important than that of nitrogen in determining the reproductive success and population dynamics of animals. Mansson and McGlade (1993) have

also scrutinized energy-based approaches to evolutionary biology and ecosystem dynamics (in particular those proposed by H. T. Odum) and concluded that there are fundamental problems in describing ecosystems using a framework that has a single currency.

Reiners (1986) has presented a more balanced, multidimensional view, proposing elemental stoichiometry as a complementary way to study questions about ecosystems that are unsuited for analysis with energy-based models. Elemental stoichiometry considers relative proportions (ratios) of key elements in organisms in analyzing how characteristics and activities of organisms influence, and are in turn influenced by, the ecosystem in which they are found. In this article we introduce the main concepts and patterns of ecological stoichiometry and synthesize literature from a variety of fields to forge connections, not only between evolutionary and ecosystem sciences but also between the disparate disciplines of cell biology and ecology. Stoichiometry may have a natural advantage in making such connections because it offers an explicit multiple-currency approach that is potentially better suited than a one-currency approach to understanding ecological and evolutionary processes that more closely resemble optimization rather than maximization (Krebs and Houston 1989).

Our approach in this article is as follows. First, we describe recent discoveries that establish the importance of consumer body

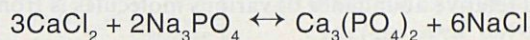
nitrogen:phosphorus (N:P) ratio in modulating secondary production and consumer-driven nutrient cycling in ecosystems. Second, we review aspects of cellular biochemistry and ultrastructure through the eyes of an ecosystem scientist, focusing on the relative nitrogen and phosphorus contents of important biomolecules and cellular structures. Third, we present examples of how organismal characters such as growth rate and ontogeny are linked with biochemical and cellular investment and thus with body N:P ratio. Finally, we propose a general scenario for allometric variation in body N:P ratio among consumers ranging from bacteria to large vertebrates and use the scenario to predict patterns of consumer-driven nutrient cycling and food quality constraints. In the spirit of Reiners (1986), we employ stoichiometric theory as a complementary approach to the study of biological processes, one that we hope will both reinforce conclusions derived from energetic perspectives as well as provide new insights into biological phenomena that may be puzzling when considered from more traditional single-currency approaches.

Ecological stoichiometry: basic concepts and patterns

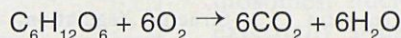
Ecological stoichiometry focuses on the relative elemental composition of participants in ecological interactions in ecosystems. Constraints of mass balance must be met both in simple inorganic chemical reactions (Figure 1a) and more complex biochemical transformations (Figure 1b); ecological interactions such as competition, predation, or herbivory are also not exempt from thermodynamics (Figure 1c). Thus, in the "ecological play," firm predictions can be made about elemental ratios in the "players" and their "stage" (sensu Lotka 1924) before and after ecological interactions.

One of the best-developed stoichiometric approaches in ecology is resource ratio competition theory (Tilman 1982). This theory, a modification of the graphical approaches of MacArthur (1972), predicts outcomes of competition for inorganic nutrients among autotrophic taxa

a Stoichiometry in chemistry



b Stoichiometry in biology (respiration)



c Stoichiometry in ecology (predator-prey interaction with nutrient recycling)

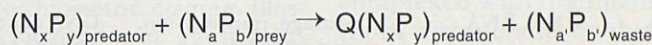


Figure 1. The first law of thermodynamics dictates mass balance of multiple elements before and after: (a) inorganic chemical reactions, (b) simple biochemical transformations (e.g., respiration of glucose), and (c) complex ecological interactions (e.g., predation with nutrient recycling). In the stoichiometry of predator-prey interactions, a prey item of a given elemental composition is consumed by a predator of fixed elemental composition to increase predator biomass by a factor Q, simultaneously producing waste of altered elemental composition. (That is, a':b' may be greater or less than a:b, depending on the relative demands for nitrogen and phosphorus required for producing predator biomass; see Sterner 1990.) The elemental ratio of recycled nutrients (a':b') contributes to the stoichiometry of another ecological interaction—nutrient competition among autotrophs in the ecosystem.

differing in elemental requirements. In competitive situations, variation in nutrient supply ratios tips the competitive balance in favor of taxa best suited to the supply regime, altering the elemental composition of autotroph community biomass and of the residual chemical environment. Resource ratio theory has been widely supported by studies of competition among autotrophs (Sommer 1989, Tilman 1982). However, stoichiometric approaches have rarely been applied to higher levels in food webs. In this article we highlight studies of elemental ratios in consumers and how they may help in understanding the role of consumers in nutrient cycling and food webs.

Consumer-regulated nutrient cycling is increasingly attracting the attention of ecosystem scientists (DeAngelis 1992, and papers in Naiman 1988) who have traditionally focused on processes mediated by autotrophs and microbes. In recent studies of consumer-driven nutrient recycling in lakes, ecological stoichiometry explains unexpected effects of food web alterations on nitrogen and phosphorus availability (Sterner et al. 1992) and identifies qualitative differences in zooplankton-phytoplankton interactions that occur in marine and freshwater habitats (Elser and Hassett 1994).

These studies have focused on species-specific differences in body N:P ratio of zooplankton that dramatically affect the relative rates of recycling of nitrogen and phosphorus by elementally homeostatic consumers (Sterner 1990). For example, when the food web structure favors dominance by consumers with high body N:P (e.g., calanoid copepods, with body N:P ratio greater than 30:1; all ratios are given as atomic ratios), then the N:P ratio of nutrients recycled by those consumers is low because food items tend to have lower N:P ratios than consumers, which would therefore tend to retain nitrogen and release phosphorus (see Figure 1c). Under such conditions, phytoplankton growth is limited primarily by nitrogen. By contrast, when fish predation on zooplankton is low, permitting dominance by low N:P taxa (especially *Daphnia*, with N:P ratio approximately 12:1), recycling N:P ratio is high and phytoplankton are phosphorus limited (Sterner et al. 1992). Thus, body N:P ratio is critical for understanding nutrient cycling in ecosystems because body N:P ratio directly determines the relative ratios of limiting nutrients recycled by consumers.

Variation in body N:P ratio is also useful in understanding a relatively new aspect of consumer ecology: the

Table 1. Major categories, examples, and biological functions of nitrogen- and phosphorus-containing molecules. General information about structure, function, composition, and relative abundance of various molecules is from Lehninger et al. (1993).

Class of molecule	Examples	Functions	Comments
Protein	Collagen, actin	Structure, regulation, communication	Average nitrogen content of the 20 amino acids in proteins is 17.2%
Nucleic acids	DNA, RNA	Storage, transmission, and expression of genetic information	DNA content (as a percentage of cell mass) conservative. RNA:DNA greater than 5:1.
Lipids	Phospholipids, glycolipids	Cell membranes	Carbon-rich, minor component of cells (approximately 5% of total cell mass)
Phosphorylated energy storage compounds	ATP, phosphocreatine	High-turnover energy carriers	ATP only approximately 0.05% of invertebrate body mass (DeZwinn and Thillart 1985)
Structural carbohydrates	Chitin	Structural support, protection	

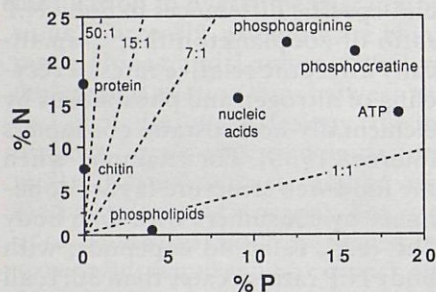


Figure 2. Stoichiometric diagram illustrating the nitrogen and phosphorus composition of biomolecules containing nitrogen and phosphorus. Values for percentage nitrogen and percentage phosphorus are given in terms of weight. Dotted lines depict standard values of atomic (molar) N:P ratio for the purpose of comparing various graphs.

role of mineral food quality in influencing consumer growth and reproduction. Mineral nutrition has traditionally been of interest primarily to managers of livestock and game animals (McDowell 1992). However, recent studies of mineral nutrition of freshwater zooplankton indicate that mineral limitation, in particular phosphorus deficiency, may be commonplace in pelagic ecosystems (Elser and Hassett 1994, Sterner and Hessen 1994). In particular, zooplankton taxa with high

phosphorus demands for growth (e.g., *Daphnia*) experience reduced growth and reproductive output when feeding on phosphorus-deficient food (Sterner and Hessen 1994). Knowledge of consumer N:P could be critical in identifying taxa most likely to suffer phosphorus limitation in nature and in assessing the extent to which the elemental stoichiometry of available food is likely to affect production of higher trophic levels.

The stoichiometric approaches just described are largely phenomenological, relying on direct measurements of body N:P ratio of dominant consumer taxa (Andersen and Hessen 1991). Observations of strongly contrasting body N:P ratios between taxa raise the question "What causes variation in body N:P?" In biology, answers to that question are of two types (Mayr 1961): proximate (biochemical and physiological) and ultimate (evolutionary). Reiners (1986) addressed both issues by distinguishing between basic "protoplasmic life," which he argues has a standard chemical stoichiometry, and "mechanical structures" (adaptations for specific functions, such as spines for defense or bones for support), which are highly variable in their stoichiometry. Thus,

selection for certain mechanical structures in functionally dominant species will alter material cycling, including global ecosystem processes.

However, we believe that there is no characteristic elemental content of "protoplasmic life" and that even unicellular organisms exhibit considerable variation in elemental ratios as a function of their evolved traits. We therefore propose that major changes in organism life history (especially size and growth rate) require substantial changes in the complement of cellular components. Because different cellular components generally have contrasting biochemical constituents that differ strongly in elemental composition, major macroevolutionary patterns must be accompanied by changes in organism stoichiometry. In the following, we focus on the limiting elements nitrogen and phosphorus and the role of heterotrophs (organo-heterotrophic bacteria, protozoa, and multicellular animals) in cycling of those elements. We explore how relationships between major life history traits and cellular organization are reflected in body N:P ratio and thus how evolved characters affect material cycling by consumers at the level of the ecosystem.

How an ecosystem scientist sees cells

Understanding how selection on major life history traits alters elemental content requires an understanding of the biochemical functions of the various molecules used by organisms and an appreciation of their elemental (especially nitrogen and phosphorus) composition. We review the function and structure of important biomolecules, summarize their relative nitrogen and phosphorus content, and then consider the biochemical and elemental composition of the cellular and subcellular structures constructed from these molecules. As ecosystem scientists, we focus on biomolecules that contain relatively large amounts of nitrogen and phosphorus and also contribute substantively to the cellular and extracellular make-up of organisms. This treatment is therefore a simplification of the actual variety of biochemicals in organisms.

Biochemical stoichiometry. Major functional classes of organic molecules used in biological systems are listed in Table 1, along with their relative nitrogen and phosphorus composition. For purposes of understanding body N:P ratios, we can neglect most carbohydrates and storage lipids because most of these contain no nitrogen or phosphorus (but see chitin, a structural carbohydrate; Figure 2). Nitrogen-rich molecules include proteins, nucleic acids, and high-energy adenylates (ATP). Note that these three classes of compounds differ little in terms of the percentage of nitrogen (Figure 2); thus, cellular structures or organisms with differing protein:nucleic acid ratios will not differ substantially in their percentage of nitrogen. The main classes of phosphorus-rich molecules (Table 1) are high-energy adenylates (particularly ATP) and nucleic acids (DNA, RNA). Due to their high phosphorus content, these molecules have low N:P ratio (Figure 2). The ATP content of organisms is generally low; thus the contribution of phosphorus from ATP to whole-organism phosphorus is also likely to be low. For example, a study of the ATP content of 22 invertebrate species (DeZwinn and Thillart 1985) indicated that phosphorus in ATP as a percentage of dried weight varies from 0.02% to 0.2%, with a mean of 0.05%. Because whole-organism phosphorus content generally ranges from 0.2% to 2%, ATP contributes little more than a fifth of whole organism phosphorus.

The molecules likely to dominate cellular and organismal N:P stoichiometry are thus proteins, due to their high nitrogen content and their substantial contribution to biomass, and nucleic acids, due to their high nitrogen and phosphorus content and their relatively high abundance. More specifically, the strong contrast in N:P stoichiometry between proteins and nucleic acids reflects the high phosphorus content of nucleic acids and indicates that a critical determinant of N:P stoichiometry of cellular structures and whole organisms will be the relative abundance of proteins versus nucleic acids.

Cellular stoichiometry. Now consider how major biomolecules are

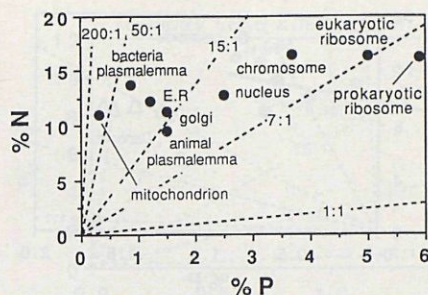


Figure 3. Stoichiometric diagram illustrating the nitrogen and phosphorus composition of major organelles and other cellular structures. Values for percentage nitrogen and percentage phosphorus are given in terms of dry weight percentage. Dotted lines depict standard values of atomic N:P ratio. As described in the text, values for elemental composition were calculated on the basis of reported biochemical composition for each structure, with the exception of nuclei and mitochondria, for which data are based on direct determinations of percent nitrogen and percent phosphorus (Bowen 1979).

deployed in cells, and thus how structures performing specific cellular processes themselves differ in biochemical and elemental composition, with potential consequences for ecosystem processes affected by body N:P stoichiometry.

Cell membranes. In both prokaryotes and eukaryotes, membranes form selectively permeable physical boundaries of compartments whose composition can be regulated to permit efficient biochemical processing (Evans 1989). Membranes consist primarily of a phospholipid bilayer and associated proteins, with a biochemical composition of 25%–56% lipids, 25%–62% proteins, and 10% carbohydrates (Frausto da Silva and Williams 1991). Thus, membrane percent nitrogen and percent phosphorus are also variable (% N: 5.2–11.1; % P: 1.1–2.4), as is membrane N:P ratio (4.9–23:1; average presented in Figure 3). Although membrane types differ in nitrogen and phosphorus content, increasing membrane contribution to overall cellular biomass would generally drive the N:P ratio down due to the phosphorus-rich phospholipid component. However, the relatively small interspecies differences in contributions of phospholipids to total body mass that have been documented

(e.g., Reinhardt and Van Vleet 1986) appear unlikely to contribute greatly to differences in organism N:P ratio.

Nucleus and chromosomes. The nucleus is the largest organelle in eukaryotic cells and consists of chromosomes, nuclear membrane with externally situated ribosomes, and proteinaceous nucleoplasm matrix. In eukaryotic chromosomes, DNA is complexed with organizing proteins (both histone and nonhistone) into chromatin, which has a protein:DNA ratio of 1–2:1 by weight (Lehninger et al. 1993). Assuming that chromatin proteins are 17.2% N by weight (above) and are present in a 1.5:1 ratio by weight with DNA, eukaryotic genetic material is thus 16.5% N by weight and 3.6% P by weight, with an atomic N:P ratio of approximately 10:1 (Figure 3). The variable complex of materials other than chromosomes in nuclei complicates calculation of the elemental composition of nuclei as a whole. However, cell fracture studies (Bowen 1979) have directly measured the nitrogen and phosphorus composition of nuclei as approximately 12.6% N and 2.5% P (N:P ratio of approximately 11:1; Figure 3).

Ribosomes. Ribosomes are sites of protein synthesis and thus are centrally involved in growth. Ribosomes are composed of ribosomal RNA (rRNA) and protein in ratios of 1.22:1 for eukaryotes and 1.8:1 for bacteria (Campana and Schwartz 1981). Calculations of elemental content based on these data indicate that ribosomes are a particularly phosphorus-rich cellular constituent (eukaryotic ribosomes: 16.3% N, 5.0% P, N:P approximately 7.2:1; prokaryotic ribosomes: 16.1% N, 5.6% P, N:P approximately 6:1; Figure 3). Because ribosomes appear to have lower N:P ratio than other subcellular structures, increasing ribosomal content will tend to lower the N:P ratio.

Mitochondria. Mitochondria are sites of oxidative ATP generation by respiration in eukaryotic cells. Mitochondria are composed of outer and inner membranes and a gel-like inner compartment known as the matrix. The matrix is approximately 50% protein by weight and also contains DNA (approximately 15,000 base pairs in human mito-

chondria) and ribosomes (Becker 1986). The outer membrane contains nearly equal proportions of lipids and proteins, whereas the inner membrane is nearly 80% protein and only approximately 20% lipid by weight (data for liver mitochondria; Lehninger et al. 1993). Convoluted foldings of the inner membrane increase its surface area, enhancing mitochondrial ATP generation. Not surprisingly, the surface area of the inner membrane correlates with the intensity of tissue respiration (Lehninger et al. 1993). Cells that respire heavily have a larger percentage of inner mitochondrial membrane, which by virtue of its high protein content has a high percent nitrogen and a high N:P ratio, than cells with smaller respiratory demands. Thus, mitochondria probably have an inherently high N:P ratio. Direct observation supports this suggestion: data for percent nitrogen and percent phosphorus from cell fracture studies summarized by Bowen (1979) indicate a mitochondrial N:P ratio of approximately 80:1 in mammalian tissues (Figure 3). Consequently, increased mitochondrial contribution would tend to increase cellular and organismal N:P ratio.

Endoplasmic reticulum (ER) and the Golgi complex. ER is a membranous network that constitutes approximately 15% of total cell volume (Mieyal and Blumer 1981). ER is the major component of the intracellular cytocavitary network, is the organizing structure for some ribosomes (rough ER), and is involved in hydroxylation reactions, detoxification, and other metabolic transformations. ER membrane has a high protein:lipid ratio of 2.3 (Becker 1986). Thus, we estimate that ER membrane itself is 12.3% N and 1.2% P by weight and has an N:P ratio of approximately 22:1 (Figure 3). The Golgi complex mediates flows of secretory proteins from the ER to the exterior of the cell and is composed of proteins and lipids intermediate in composition between ER membrane (from which Golgi membrane is thought to arise) and plasma membrane (with which Golgi-derived secretory vesicles eventually fuse in discharging their contents to the outside of the cell;

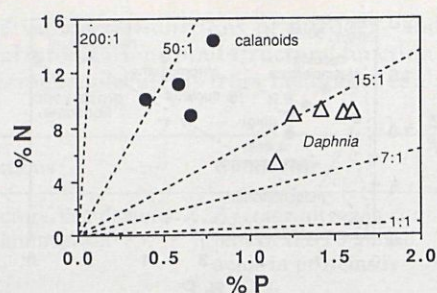


Figure 4. Stoichiometric diagram illustrating the characteristic difference in nitrogen and phosphorus composition for two major herbivorous zooplankton groups: calanoid copepods (circles; four species plotted) and the cladoceran *Daphnia* (triangles; five species plotted). Values for percentage nitrogen and percentage phosphorus are given in terms of dry weight percentage. Dotted lines depict standard values of atomic N:P ratio. Data from Andersen and Hessen (1991) and Hessen and Lyche (1991).

Becker 1986). Assigning the Golgi a protein:lipid ratio of 1.7 (intermediate between the protein:lipid ratios of plasma membrane and ER), we estimate the elemental composition of the Golgi apparatus as 11.2% N and 1.5% P, with an N:P ratio of 17:1 (Figure 3).

Cytoplasm. Cellular cytoplasm is composed of cytosol (the soluble portion of the cytoplasm) and cytoskeleton (an internal framework that gives eukaryotic cells their distinctive shape and internal organization and governs the position and movement of organelles). In typical animal cells, cytoplasm occupies more than half of cell volume. Protein content of the cytosol exceeds 20% (Lehninger et al. 1993), likely reflecting localization of the majority of enzymes of intermediary metabolism. Proteinaceous microtubules dominate the structural components of cytoskeleton (Lehninger et al. 1993). Because cytoskeleton probably contributes more to total cell mass in larger, more differentiated cells than in small, undifferentiated cells, if all else were equal we would expect such cytoskeleton-rich cells to have a higher N:P ratio.

Extracellular materials. Unicellular organisms release materials to the exterior of the plasma membrane to form cell walls, and in multicellular organisms, extracellular

materials are involved in cellular aggregation, tissue organization, maintenance of intercellular spaces, and construction of protective coverings and support structures. Thus, the biochemical and elemental composition of these materials must be considered for a complete view of organism composition. For example, invertebrates commonly use the nitrogenous polysaccharide chitin (Figure 2) for exoskeletons (insects) and carapaces (crustaceans). In vertebrates the fibrous protein collagen is the major extracellular structural protein in connective tissue and bone, making up one-third or more of total body protein in higher vertebrates (Lehninger et al. 1993). Also of critical importance in determining whole organism elemental content in vertebrates is bone itself, which is deposited as apatite [$\text{Ca}_5(\text{OH})(\text{PO}_4)_3$] within a proteinaceous connective tissue matrix (Frausto da Silva and Williams 1991). The phosphorous content of bone is sufficiently high that bone has a very low N:P ratio (0.8:1) despite the importance of collagen in the bone matrix.

Organismal N:P ratio and life history characters

Primary life history parameters of organisms, especially specific growth rate, are linked to biochemical composition and body N:P stoichiometry. We focus on crustacean zooplankton, the group with which we are most familiar, but data for other groups illustrates how these linkages are general across broad taxonomic and habitat categories.

Growth rate and N:P stoichiometry. Studies of nitrogen and phosphorus composition of zooplankton have revealed patterns (both within and between taxa) that are particularly instructive in understanding links between elemental composition, biochemical makeup, and life history strategies. The two dominant groups of crustacean herbivores in freshwater plankton, calanoid copepods and cladocerans, have contrasting life histories. Cladocerans (e.g., *Daphnia*) grow rapidly, reach sexual maturity (for parthenogenetic reproduction) within days of birth under good food conditions, and produce

many generations within a growing season. Calanoid copepods, by contrast, grow slowly, reproduce sexually, and generally complete only one or two generations during a year. In addition, copepods undergo complex metamorphosis, whereas cladocerans do not.

Large differences in body N:P ratio accompany these life history contrasts (Figure 4). Both marine and freshwater calanoid copepods have N:P ratios exceeding 30:1 (Andersen and Hessen 1991, Båmstedt 1986, Hessen and Lyche 1991). However, cladocerans, a predominantly freshwater group, have an elemental composition with slightly less nitrogen and considerably more phosphorus, resulting in lower N:P ratios (12–18:1; Andersen and Hessen 1991, Baudouin and Ravera 1972, Hessen and Lyche 1991). For example, *Daphnia* has an N:P ratio of 15:1 (Figure 4). However, carnivorous cladoceran species seem to have higher N:P ratios than herbivorous cladocerans of similar size (Hessen and Lyche 1991).

Although data are limited, the biochemical basis of the differences in body N:P ratio between cladocera and copepods is becoming clear (Sterner 1995, Sterner and Hessen 1994). First, nitrogen composition varies from only 8%–10% in both copepods and cladocerans (Andersen and Hessen 1991, Hessen and Lyche 1991). Because nitrogen is a primary constituent of proteins, it is likely that the protein pool varies little across taxa. In contrast, the specific phosphorus content of zooplankton is apparently much more variable: the mean percentage phosphorus values for copepods and cladocerans (especially *Daphnia*) are less than 0.6% and around 1.5%, respectively (Andersen and Hessen 1991, Baudouin and Ravera 1972, Hessen and Lyche 1991). As discussed above, phosphorus is a constituent of several prominent biochemicals in cells: phospholipids, ATP/ADP, and nucleic acids. Phospholipids are a minor constituent in cells, and high-energy adenylates likewise generally contribute less than 1% to dry weight in zooplankters (Båmstedt 1986). This leaves nucleic acids as the remaining candidate to explain variation in percent phosphorus among

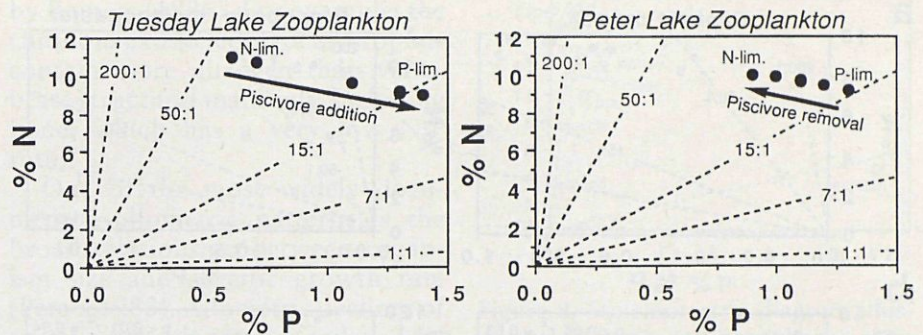


Figure 5. Stoichiometric diagram illustrating changes in estimated nitrogen and phosphorus composition of zooplankton communities during food web manipulations (introduction or removal of piscivorous bass) reported by Elser et al. (1988). Dotted lines depict standard values of atomic N:P ratio. Values for percentage nitrogen and percentage phosphorus are given in terms of dry weight percentage. Estimates of zooplankton community N:P stoichiometry were made using data for biomass contribution of copepods and *Daphnia* and published values of percentage nitrogen and percentage phosphorus for these groups (see Figure 4). Data points indicate weekly observations during periods of rapid zooplankton change. Shifts in the nature of phytoplankton nutrient limitation (nitrogen versus phosphorus) as a result of changes in zooplankton community N:P stoichiometry are indicated. Tuesday and Peter Lakes are located at the University of Notre Dame Environmental Research Center in Michigan's upper peninsula.

taxa. In fact, copepods are generally around 2% RNA by weight, whereas *Daphnia* can be as high as 10% RNA (Båmstedt 1986, Baudouin and Scoppa 1975, Dagg and Littlepage 1972, McKee and Knowles 1987). Assuming that RNA is 10% phosphorous (Figure 2), the entire difference in specific phosphorus content of these zooplankton groups (0.8% phosphorous) can be explained by differences in RNA content (Sterner 1995).

This example provides one of the best illustrations of the fundamental link between organism life history, biochemical investment, and body stoichiometry. Cladocerans in general, and *Daphnia* in particular, have evolved traits that favor rapid growth and high reproductive output, whereas copepods grow more slowly and live longer. *Daphnia*'s high growth rate requires a high ribosomal complement for extensive protein synthesis coupled to that high growth rate. Thus, its tissues have high rRNA and therefore high phosphorus contents and low N:P ratio, making *Daphnia* a poor recycler of phosphorus relative to nitrogen.

We can now see the study of Elser et al. (1988), the first to document qualitative effects of consumers on availability of nitrogen and phosphorus in ecosystems, in a new light.

In Tuesday Lake, predation pressure on zooplankton was reduced by introducing piscivorous bass that reduced zooplankton-feeding minnow populations. *Daphnia* (a superior competitor to copepods by virtue of its high grazing and growth rates) rapidly came to dominate the zooplankton, replacing calanoid copepods (Figure 5). The replacement of high N:P copepods with low N:P *Daphnia* likely produced a high recycling N:P ratio. Thus, the same feature that enables *Daphnia* to achieve dominance under low predation (its rapid growth rate) necessitates investment in biochemical and cellular machinery that lowers body N:P ratio (Figure 3) and elevates recycling N:P ratio in the ecosystem (Figure 5). Conversely, when nearby Peter Lake was manipulated to increase predation intensity on *Daphnia*, slower growing zooplankton species (calanoid copepods and small cladocerans) achieved dominance and, by virtue of their reduced investment in low N:P cellular constituents, generated a low recycling N:P ratio (Figure 5). Such variations in recycling N:P ratio as a function of consumer N:P ratio are now becoming more widely documented (Elser and Hassett 1994, Elser et al. 1995, Urabe 1993, Urabe et al. 1995).

In addition to these nutrient cy-

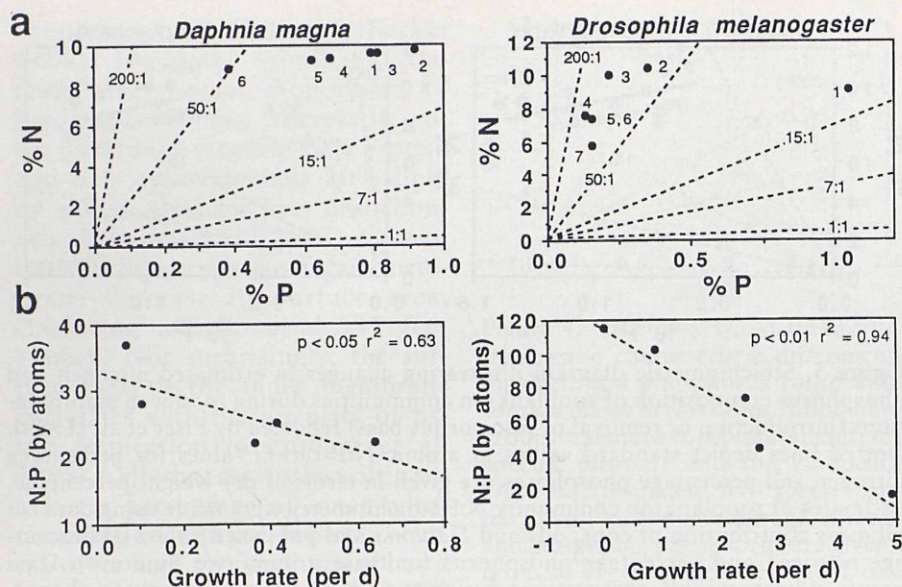


Figure 6. (a) Stoichiometric diagrams illustrating ontogenetic variation in percentage nitrogen and percentage phosphorus in *Daphnia magna* and *Drosophila melanogaster*. Dotted lines depict standard values of atomic N:P ratio. Values for percentage nitrogen and percentage phosphorus are given in terms of dry weight percentage. Numbers indicate the ontogenetic sequence of the observations. (b) Correlation between body N:P ratio and specific growth rate during ontogeny in *D. magna* and *D. melanogaster*. Data for *D. magna* are from McKee and Knowles (1987) and for *D. melanogaster* are from Church and Robertson (1966).

clinging effects, researchers are beginning to explore how the nutritional value of food (specifically food phosphorous content) alters how consumers with different life histories and N:P stoichiometries respond to changes in food web structure. For example, we recently manipulated the food web of a severely phosphorus deficient lake on the Canadian Shield in Ontario by introducing predatory pike to a minnow-dominated food web lacking *Daphnia*. Despite 100-fold reductions in minnow abundance, *Daphnia* increases have been modest and high N:P calanoid copepods remain dominant,¹ suggesting that the poor quality of the lake's severely phosphorus limited phytoplankton prevents dominance by low N:P *Daphnia*. Body stoichiometry thus provides a framework to establish direct mechanistic links between the molecular processes of growth at the level of the cell and the reciprocal interactions between organisms and the ecosystems in which they are found.

¹J. J. Elser, T. H. Chrzanowski, R. W. Sterner, and K. H. Mills, 1996, manuscript in review.

Ontogeny and N:P stoichiometry. Many organisms undergo complex developmental sequences (ontogeny) during which both body size and specific growth rate vary considerably. Thus, we would also expect variation in biochemical and elemental composition to accompany ontogeny. To the extent that N:P stoichiometry changes during development we would also expect variation in an organism's effects on nitrogen and phosphorus cycling and its sensitivity to mineral food quality.

Data on biochemical composition and specific growth rate during ontogeny in a variety of invertebrates show that there are indeed strong ontogenetic shifts in body stoichiometry. For example, daphnids appear to maintain high concentrations of RNA throughout ontogeny, resulting in modestly variable but generally low N:P ratios in all life stages (Baudouin and Ravera 1972, McKee and Knowles 1987; Figure 6a). In contrast, complex metamorphosis in copepods appears to result in more dramatic changes in elemental composition during ontogeny. Protein:RNA ratio in copepod nauplii (stages

immediately following hatching) is low (and thus body N:P ratio is low); as development progresses through copepodid (juvenile) stages, growth rate slows and investments in structural proteins increase, causing increases in the protein:RNA ratio (Båmstedt 1986, Dagg and Littlepage 1972) and thus in N:P ratio. Thus, effects of individual copepods on relative nitrogen and phosphorus cycling in nature probably vary strongly during development.

Strong shifts in body biochemical and elemental composition during development are not confined to copepods. Holometabolous terrestrial insects exhibit similar trends in biochemical and elemental composition (Church and Robertson 1966, Lang et al. 1965). For example, body N:P ratio of *Drosophila melanogaster* varies from 9:1 in early larvae to 100:1 immediately before pupation (Church and Robertson 1966; Figure 6a). Variation in body stoichiometry during ontogeny also provides compelling evidence that the main determinant of body N:P in invertebrates is specific growth rate: stage-specific body N:P ratio is strongly ($r^2 > 0.85$) and linearly correlated ($P < 0.01$) with stage-specific growth rate in both *Daphnia* and *Drosophila* (Figure 6b).

Organism size and N:P ratio: a prediction

We have discussed how evolved characteristics, such as growth rate and developmental sequences, translate into differences in biochemical and elemental composition in consumers. In this section we discuss how macroevolutionary patterns in life history traits also have implications for organismal N:P stoichiometry, focusing on the central parameter of traditional life history theory, organism size. How does body N:P ratio in healthy, actively growing organisms vary in consumer taxa ranging from bacteria (less than 1 picogram [pg]) to large vertebrates (7000 kg or more), a size range of 15 orders of magnitude? The study of allometry in body stoichiometry has considerable potential for new insights into the causes and consequences of evolutionary processes in consumer taxa. These insights may

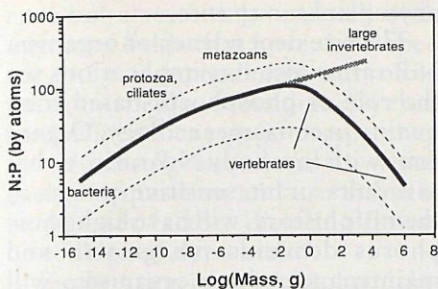


Figure 7. Predicted variation in organism N:P ratio (by atoms) as a function of organism size (g dry weight). Dotted lines above and below the main trend (black line) are meant to indicate that there is likely to be important ecologically or evolutionarily derived variation in organism N:P ratio at any given body size. For large organisms, two trajectories are possible. One trajectory (gray line) corresponds to a continuous increase in organism N:P ratio (which is likely for large invertebrates) and the other to a decline in organism N:P ratio due to increasing bone investment in vertebrates (the main group of animals of large body size).

complement those that have resulted from a widespread study of allometry in energetic relations (Schmidt-Nielsen 1984) in consumers.

The question of whether organismal N:P ratio varies significantly and systematically with size distills to whether percent nitrogen and percent phosphorus vary differently with body size. We have already shown that, within certain taxa, percent nitrogen and percent phosphorus are clearly not isometric, because the body N:P ratio varies ontogenetically, and therefore with size, in *Daphnia magna* and, especially, *D. melanogaster* (Figure 6a). But what about allometric variation across taxa?

Two factors probably influence organism N:P ratio as we proceed from bacteria to large vertebrates. First, the biochemical and elemental composition of protoplasm may vary significantly with size. For example, organisms adapted for rapid growth may contain a greater proportion of RNA, and thus have a lower N:P ratio, than organisms adapted for slower growth. The second factor influencing the size-dependence of body N:P is that increases in size may bring concomitant increases in structural materials, as emphasized

by Reiners (1986). For example, the chitinous exoskeletons of arthropods contain more nitrogen than vertebrate structural materials, including bone, which has a very low N:P ratio.

One of the most widely documented allometric patterns is the broad relationship between organism size and specific growth rate (Peters 1983). Allometric declines of specific growth rate (as indexed by production per unit biomass) with size have similar slopes (approximately -0.25) for unicells, poikilotherms, homeotherms, tetrapods, mammals, and fish, although in some cases the intercepts are displaced somewhat and the slope of the relationship for invertebrates is steeper (-0.37). These patterns hold within more specific taxonomic categories as well. For example, in ciliates specific growth rate declines significantly with cell volume (Fenchel 1968).

If the link between organism N:P ratio and specific growth rate (Figure 6) is general, it follows that as organisms increase in size, the organismal N:P ratio should increase (Figure 7). This view is supported by available but extremely limited data. For example, healthy bacterial cells (mass: 1 pg) have extremely rapid growth rates and can have N:P ratio as low as 5:1 (Bratbak 1985). The small flagellate *Paraphysomonas imperforata* (mass: 5 nanogram [ng]) has an N:P ratio of 10:1 (Caron et al. 1985), whereas characteristic N:P ratios for crustacean zooplankton in the 10–100 μg range are generally 12–70:1 (Andersen and Hessen 1991) and those for late instar *Drosophila* larvae (mass: 0.5 mg) are 100:1 (Figure 6a). Variation around this general pattern is likely. For example, the different N:P ratios of the similarly sized crustacean zooplankters *Daphnia* and calanoid copepods (12:1 versus greater than 30:1) probably reflect differences in their specific growth rates. Thus, just as allometric patterns of growth rate with body size show considerable scatter, we would also expect to observe substantial deviations from the overall trend of increasing N:P ratio with organism size over this size range. These deviations are likely to have significant evolutionary and ecologi-

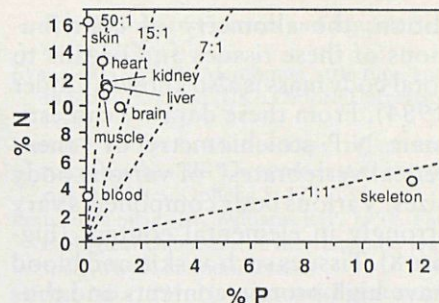


Figure 8. Stoichiometric diagram illustrating nitrogen and phosphorus composition of mammalian organs and organ systems. Dotted lines depict standard values of atomic N:P ratio. Values for percentage nitrogen and percentage phosphorus are given in terms of dry weight percentage. Data from Bowen (1966).

cal causes, as in the case of *Daphnia* versus copepods.

However, the trend of increasing organism N:P ratio with increasing body size is unlikely to continue monotonically throughout the complete range of organism size because other factors, in particular structural investments, come into play at large organism size. In particular, vertebrates, which enter the size continuum at around 100 mg, complicate the picture because contributions of skeletal materials are likely to strongly influence whole organism N:P ratio. Thus, for large organisms, it is necessary to consider how protoplasmic and structural components combine to affect organismal N:P ratio. For both invertebrates and vertebrates of large body size, specific growth rate declines with body size (Peters 1983). Indeed, specific RNA content is known to decline with body size in certain mammalian tissues (Peters 1983). So, N:P ratio of large invertebrate biomass and of "soft-tissue" biomass of vertebrates likely continues to increase with size. However, the structural support investments of vertebrates begin to dominate body N:P ratio and necessitate a different approach to predicting size dependence of N:P ratio within the vertebrates, the dominant group of organisms larger than 10 g.

Evaluating N:P ratio at large body size is facilitated by information on the biochemical and elemental composition of major tissues and organs of vertebrates (Bowen 1966). In ad-

dition, the allometry of contributions of these tissues and organs to total body mass is also known (Calder 1984). From these data we can estimate N:P stoichiometry of "theoretical vertebrates" of various body sizes. Various body components vary strongly in elemental content (Figure 8). Tissues such as skin and blood have high protein contents and thus have high N:P ratio (greater than 100:1); in contrast, skeletal material is phosphorus rich due to the deposition of apatite within collagen-based connective tissue (Frausto da Silva and Williams 1991) and has low N:P ratio (0.8:1). The relative contributions of various tissues vary strongly with body size; data for mammals were analyzed by Calder (1984). Of particular interest in this context is an increase in percent skeletal mass with body size from 3.8% of body mass in shrews to 13.6% in elephants (Prange et al. 1979).

To evaluate N:P variation with body size in vertebrates, we used percent nitrogen and percent phosphorus data for various organ systems compiled by Bowen (1966) as fixed values (although they likely vary with body size as well; see discussion above) and calculated body percent nitrogen and percent phosphorus based strictly on Calder's (1984) equations regarding contributions of tissue and organ systems as a function of body size. These calculations predict a strong size dependence for N:P stoichiometry within vertebrates: we estimate that a 10-g vertebrate is 10.8% N and 0.98% P (N:P ratio: 24:1), whereas a 1000-kg vertebrate is 7.0% N and 1.6% P (N:P ratio: 9.6:1).

The substantial shifts in organism N:P ratio with size (Figure 7) have implications for impacts of consumers on ecosystem nutrient cycling. The increase in organism N:P ratio from bacteria through metazoans implies that larger organisms within this size range will generally be more efficient recyclers of phosphorus than of nitrogen. Relative recycling efficiencies for nitrogen and phosphorus by a consumer depend on the N:P ratios of both prey and consumer (Sterner 1990); thus, the degree to which the consumer differentially recycles nitrogen and phosphorus will be determined by the size dichotomy

between predator and prey. Because predators are generally larger than their prey, the increasing N:P ratio with organism size implies that elemental imbalance (food N:P ratio - consumer N:P ratio; Elser and Hassett 1994) will generally be negative for consumers eating other consumers and thus will result in a low recycling N:P ratio. This is in strong contrast to the interaction between herbivorous consumers and primary producers (which commonly have extremely high N:P ratios); elemental imbalance for the herbivore-producer interaction is frequently strongly positive in lakes, resulting in high recycling N:P ratio (Elser and Hassett 1994).

Decreases in N:P ratio with large body size also probably influence direct effects of large animals on nutrient cycling, an impact that has been increasingly emphasized (Naiman 1988). For example, many studies have shown that migration of anadromous fishes from oceans to lakes, where adults spawn and die, represents a significant source of phosphorus to the lake (Northcote 1988). The low N:P ratio of large vertebrates (Figure 7), including fish (e.g., body N:P ratio of northern pike [*Esox lucius*] is around 12:1 [George 1994]), implies that such fluxes differentially introduce phosphorus (relative to nitrogen) to lakes. Moreover, Carpenter et al. (1992) have shown that fish transport phosphorus from the littoral zone (where they capture prey) to the pelagic zone (where they excrete wastes). However, most studies of fish nutrient cycling have focused exclusively on phosphorus and have not considered nitrogen (but see Vanni 1995).

Our predictions of N:P ratio (Figure 7) indicate that fish have body N:P ratios lower than those of most of their prey (size range: 50 μ g-1 g). Thus, stoichiometry predicts that fish should differentially recycle nitrogen relative to phosphorus (Sterner 1990); if fish alter the phosphorus budgets of pelagic ecosystems, then they are also likely to alter the nitrogen budgets even more strongly. Thus, an indirect effect of fish on phytoplankton communities not yet emphasized by aquatic ecologists is an alteration of the N:P supply ratio and thereby a shift in competitive relations among

phytoplankton species.

The size dependency of organism N:P ratios also has implications for the role of phosphorus-based food quality in consumer ecology. Organisms with low body N:P ratio, either as adults or at sensitive points in their life history, will have high phosphorus demands for growth and maintenance; these organisms will thus require food that meets not only their energetic demands but also their somatic elemental demand. The recent discovery of effects of phosphorus-deficient food quality on low N:P zooplankton (e.g., *Daphnia*; Sterner and Hessen 1994) provides an intriguing complement to examples of phosphorus-based food quality constraints on vertebrate herbivores (livestock and game populations; McDowell 1992), which also have low N:P ratio. Thus, we suggest that organism N:P ratio provides a tool for identifying taxa, or key life history stages within taxa, that are most likely to be affected by variation in phosphorus-based food quality in ecosystems. This stoichiometric knowledge may lead to a better understanding of consumer foraging behavior and population regulation that may not be obtained from studies that view production and foraging solely in terms of energetic parameters.

Conclusions

We have shown how the mechanistic bases of a phenomenon occurring at the level of the ecosystem (differential recycling of nitrogen and phosphorus as affected by food web structure) can be traced to the level of the cell and molecule by focusing on N:P stoichiometry. This application of stoichiometric thinking was possible because species that are dominant under contrasting ecological conditions have contrasting life histories requiring different cellular and biochemical investments that necessarily result in differences in body N:P ratio. Elemental stoichiometry can thus provide a new tool to trace the threads of causal mechanisms linking cellular, ecosystem, and evolutionary processes. It offers a means of integrating not only the traditionally disparate disciplines of evolutionary biology and ecosystem sci-

ence but also ecology and cell biology, two fields that have developed not only independently but often antagonistically. Stoichiometry thus complements energetic perspectives by addressing situations in which energy acquisition and use may not be primary factors dictating fitness or ecological dynamics.

Exploration of the role of stoichiometry in regulation of biological processes is just beginning, even within ecology. Nevertheless, consideration of biochemical and elemental consequences of macroevolutionary trends sets the stage for a unified evolutionary view of the cellular mechanisms that drive ecosystem processes. The power of stoichiometric perspectives arises from the unavoidable demands for chemical elements and the first law of thermodynamics, which applies to all processes by which organisms are born, grow, develop, and die. The essence of this idea was also captured by the Greek philosopher-scientist, Empedocles (quoted by Lotka 1924):

There is no coming into being of aught that perishes, nor any end for it...but only mingling, and separation of what has been mingled.

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