

Ecological Stoichiometry as an Integrative Framework in Stream Fish Ecology

PETER B. MCINTYRE*

*Center for Limnology & Department of Zoology, University of Wisconsin
Madison, Wisconsin 53706, USA*

ALEXANDER S. FLECKER

*Department of Ecology & Evolutionary Biology, Cornell University
Ithaca, New York 14853, USA*

Abstract.—Ecological stoichiometry refers to the relative availability of elements in ecosystems as both an influence upon and result of ecological interactions. Nutrient ratios have long been analyzed in primary producers, but their application to animals is more recent. Here, we summarize the ecological stoichiometry framework and highlight three key contexts in stream fish ecology: body stoichiometry, dietary stoichiometry, and roles in ecosystem nutrient cycling. Elemental demands for growth depend directly upon the stoichiometry of carbon and nutrients in body tissues. Body stoichiometry varies widely among the dozens of stream fish species for which data are available and exhibits some phylogenetic and size-based patterns. Due to the variety of foods consumed by stream fishes, the stoichiometry of their diets also varies widely. Consuming foods with high carbon:nutrient ratios can produce phosphorus-limited growth in algivores and potentially in insectivores as well. These expectations contrast with the prevailing belief that energy intake is the key nutritional control on growth of most fishes. Ingested nutrients that are not incorporated into body tissues must be defecated or excreted. These waste products can be a critical component of ecosystem nutrient cycles and offer the opportunity for species identity to affect ecosystem functioning. We argue that ecological stoichiometry provides an integrative framework for merging perspectives across individual, population, community, and ecosystem levels. Broader application of this approach to stream fishes will offer particular insight into consumer–resource interactions and ecosystem dynamics.

Introduction

Ecological stoichiometry is one of the few ecological concepts that can be applied quantitatively across many levels of biological organization, thereby highlighting mechanistic linkages from individual cells all the way up to the bio-

sphere (Reiners 1986; Sterner and Elser 2002). As a consequence, theoretical and empirical work on ecological stoichiometry continues to yield insights that bridge traditional disciplinary boundaries between environmental chemistry, biochemistry, ecology, and evolutionary biology. Such integration is made possible by using chemical elements as natural currencies

* Corresponding author: pmcintyre@wisc.edu

whose pools and fluxes can be assessed at any spatial or ecological scale. The key insight of ecological stoichiometry is that the relative availability of elements determines which one most constrains ecological dynamics; all others are present in excess of potential demand and thus should not be limiting. To foster this relativistic perspective, researchers generally use elemental ratios expressed in atomic or molar units rather than by weight.

Though the concept of ecological stoichiometry has deep roots (e.g., Lotka 1925; Redfield 1958), its exploration was largely limited to plant and phytoplankton ecology until two decades ago. In the mid-1980s, a seminal essay by Reiners (1986) laid out the framework for using elemental analyses to understand patterns and processes at scales from organisms to the biosphere. In the decade that followed, zooplankton ecologists discovered that low phytoplankton nutrient content could be a constraint on herbivore growth and fitness. Specifically, they noted that differences in nutrient requirements among zooplankton species could produce differential responses to algal nutrient content (Sterner and Hessen 1994), with potential for feedbacks on ecosystem nutrient availability through nutrient recycling (e.g., Elser et al. 1988). Subsequent theoretical, experimental, and observational research has explored these questions in detail for zooplankton communities and for some lake-dwelling fishes and stream invertebrates. However, the potential for ecological stoichiometry to elucidate aspects of the ecology of stream fishes remains largely unrealized. In this chapter, we outline many ways in which ecological stoichiometry can serve as an integrative framework in stream fish ecology.

The rationale for incorporating the ecological stoichiometry perspective into research on stream fish ecology is simple—fish are the most nutrient-rich organisms in streams.

When they are abundant, fish may constitute the dominant pool of phosphorus and nitrogen in a stream ecosystem, as observed in many lakes (Griffiths 2006). The availability of these nutrients often constrains rates of primary production and organic decomposition, therefore sequestering nutrients at upper trophic levels enables fish to play a regulatory role in ecosystems by enhancing the total pool of nutrients and reducing the rate of nutrient turnover. Even when fish biomass is low, the high concentration of nutrients in their tissues relative to the rest of the stream environment has profound consequences for fish physiology, growth, and predator–prey interactions. To explore these implications, we will begin by outlining two principles at the core of ecological stoichiometry: mass-balance constraints and homeostatic regulation. With these ground rules as background, we will then discuss three key aspects of ecological stoichiometry in stream fish ecology: dietary stoichiometry, body stoichiometry, and roles in ecosystem nutrient cycling.

Ground Rules of Ecological Stoichiometry

With regard to the ecology of fishes and other animals, two key rules form the basis of the ecological stoichiometry perspective. The first is the mass-balance requirement for chemical reactions, which stipulates that quantities of reactants and products must be equal for every element. Though it seems trivial, this rule has critical implications for consumer–resource interactions. Imagine both consumer and prey not as organisms but as amalgams of numerous chemical elements. Prey serve as the reactants supplied for the reaction (S_{prey}), and the consumer's tissues are a product (P_{consumer}). When the match between the chemical composition of predator and prey is imperfect, as is typically the case, additional byproducts are required to

balance the equation. These byproducts are the wastes released by the consumer, comprising excretion of dissolved compounds (E), defecation of particulates (D), and respiration of gaseous byproducts of metabolism, such as CO₂ (R). The overall mass-balance equation is as follows: $S_{\text{prey}} = P_{\text{consumer}} + E + D + R$, where excretion and defecation are often grouped as recycling for purposes of discussion and respiration is generally ignored from the nutrient perspective. The requirement of mass balance within this equation creates clear predictions for recycling of nonlimiting elements as a function of the imbalance between fish and their food resources. Given a fixed need for an element by a fish, its recycling rate will be directly proportional to its ingestion of that element, where ingestion reflects both the quantity of food ingested and the dietary concentration of the element (Figure 1A). Alternatively, given a fixed ingestion rate of an element, a fish's recycling rate of that element will be negatively related to its demand for the element to grow new body tissues or reproduce (Figure 1B). Thus, relatively low nutrient recycling rates can reflect many different influences, including

a low-nutrient diet, low ingestion rate, rapid growth, or high body nutrient content.

When multiple elements are considered simultaneously, the balance between dietary supply and fish demands is sure to differ among elements. Agronomists and ecologists have long recognized that the element for which the supply:demand ratio is lowest limits the reaction rate because its supply is exhausted first (Redfield 1958)—this is often referred to as Liebig's law of the minimum. For consumers like fish, increased ingestion of the limiting element leads to increased assimilation of all other elements by enhancing growth or reproduction. In contrast, consuming more of a nonlimiting element has no benefits for growth and reproduction because it was already available in excess of the fish's needs.

This relativistic perspective is the crux of ecological stoichiometry and spurs a focus on elemental ratios rather than single elements (Sterner and Elser 2002). Interpreting elemental ratios requires a bit more thought. For instance, a demand ratio of X:Y means that a consumer requires amount X of the first element for every amount Y of the second ele-

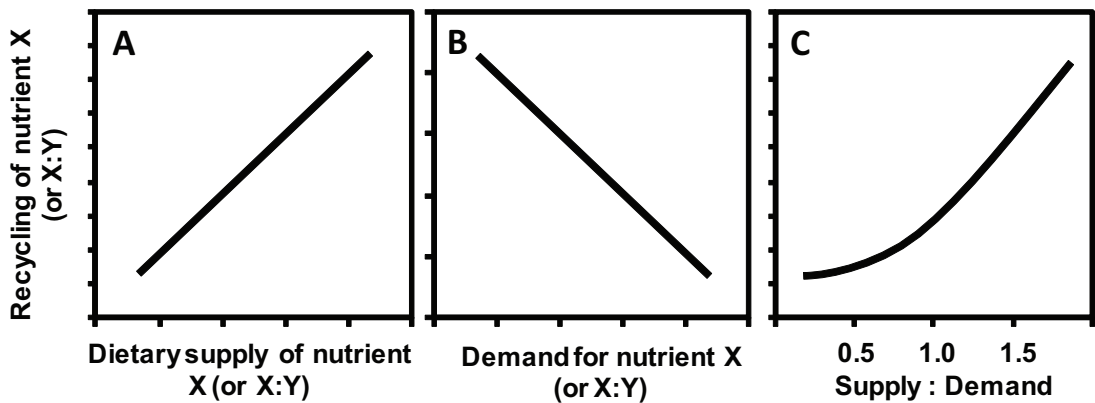


Figure 1. General predictions for recycling of dietary nutrients by stream fish as a function of (A) dietary nutrient supply when demands are less than supply, (B) nutrient demands for growth and reproduction, and (C) the supply:demand ratio. In (C), recycling shows a nonlinear pattern when demand exceeds supply (supply:demand < 1.0) because nutrient retention efficiency is expected to increase for growth-limiting nutrients. Modified from Sterner and Elser (2002).

ment used to meet its needs for growth and reproduction. Just as in the single-element case, we can compare demand and supply, but now this requires computing a ratio of two ratios, each of which features the same pair of elements in the numerator and denominator. The limiting element can be identified as the one yielding the highest ratio of the demand ratio to the supply ratio.

The mass-balance requirement also operates in this multi-element context, but can yield more interesting consequences of consumer-resource imbalances. Just as before, the ratio of recycled elements is negatively related to the demand ratio given a fixed supply ratio (Figure 1B), and the recycling ratio is directly proportional to the supply ratio as long as the demand ratio is both fixed and lower than the supply ratio (Figure 1A). However, when a consumer has a higher demand ratio than the supply ratio provided by its food, a curvilinear relationship between recycling and supply arises because the nutrient in the numerator becomes limiting (Figure 1C). For a limiting nutrient, the recycling rate (or ratio) declines ever more slowly as the supply rate gets further below demand, asymptotically approaching whatever minimum recycling rate the fish's physiology allows (Sternler and Elser 2002).

The second key rule in ecological stoichiometry is that animals exhibit relatively inflexible stoichiometry compared to plants and perhaps microbes. Though this rule represents an empirical pattern rather than an absolute requirement derived from first principles, it appears robust enough to serve as a rule for practical purposes (Sternler and Elser 2002). The consistent stoichiometry of animals reflects homeostatic regulation, wherein both the elemental composition of individual tissue types and the proportional representation of each tissue type within the body are maintained at some characteristic level. In contrast, plants generally lack homeostatic

regulation, instead taking up elements roughly in proportion to their availability. Some microbes also appear to have considerable plasticity in their nutrient content (e.g., Cotner et al. 2006). Stoichiometric plasticity allows plants and perhaps microbes to take advantage of spatiotemporal variation in the availability of elements by balancing investment in cellular machinery for growth versus resource acquisition (Klausmeier et al. 2004). For fishes, the chief implication of stoichiometric variation in plants and microbes is that these organisms vary widely in their value as food resources, whereas a diet of invertebrates or other fish provides a more predictable source of nutrition. At the same time, the stoichiometric inflexibility of fishes due to skeletal investment and other fundamental needs creates the potential for their growth and reproduction to be limited by nutrients rather than energy or other factors.

We will review the evidence for homeostatic regulation of fish body stoichiometry in the next section, but first we must be careful to recognize the difference between the composition of body tissues and the net demand for various elements by a living fish. This distinction is minor in the case of ratios of multiple nutrients, but carbon:nutrient ratios in body tissues are considerably lower than those required by a fish to survive. The difference arises from the high demand for carbon relative to nutrients in order to support basal metabolism (Anderson et al. 2005). Thus, a fish that neither grows nor invests in gametes will have minimal nutrient requirements, yet its demand for carbon may be quite high. Moreover, differential demand for various nutrients during maintenance versus growth can dramatically alter nutrient recycling ratios of fish (Schindler and Eby 1997).

With an understanding of the constraints imposed by mass balance and homeostatic regulation of stoichiometry, we will now review the literature on the stoichiometry of

fishes themselves, of their diets, and of recycled wastes. Each of these three components of the mass-balance equation varies widely, and our overview will emphasize the implications of this variation for the ecology of stream fishes and their roles in ecosystem functioning. Our discussion will focus upon just three elements—carbon (C), nitrogen (N), and phosphorus (P)—that have received a large majority of the attention in stoichiometric research. Carbon is the essential constituent of all organic materials and makes up more of the dry mass of organisms than any other element. Nitrogen is the key nutrient required for proteins and some structural materials (e.g., chitin) and also makes up a substantial proportion of organism mass. Phosphorus is required in relatively small amounts, but ambient concentrations are disproportionately low such that P availability often limits primary production in freshwater ecosystems, including some streams (Dodds 2007). Though future research on ecological stoichiometry will likely encompass many more elements, analyses focused on C, N, and P illustrate the value of a stoichiometric perspective for understanding many aspects of stream fish ecology.

Body Stoichiometry of Stream Fishes

Though individual fish may regulate their body stoichiometry in a homeostatic fashion, this does not mean that all fish species have equivalent composition. To the contrary, analyses of fish body nutrient content reveal that species differ widely in their content of various elements, particularly phosphorus. Recent work, some of it dealing with species found in streams, has begun to elucidate the range of stoichiometric variation as well as the causal basis for intra- and interspecific differences.

To summarize the body C, N, and P content of freshwater fishes, we compiled published

records (Penczak 1985; Penczak et al. 1985; Sterner and George 2000; Tanner et al. 2000; Vanni et al. 2002; Hendrixson et al. 2007; Dantas and Attayde 2007) and our unpublished data on species from Rio Las Marias, Venezuela. The resulting data set encompassed 100 species from 31 families. Half of these were temperate species from North America and Europe, and the other half are tropical species from South America. Temperate cyprinids were best represented (20 species), followed by tropical characids (12 species). Fifteen families were represented by a single species. When multiple conspecific populations were studied within one or more studies, we used the average value weighted by sample size. We did not include the data of Davis and Boyd (1978) because its accuracy is suspect (Griffiths 2006). For further analysis, each species was assigned to a trophic guild (algivore, invertivore, piscivore, detritivore, generalized carnivore, and omnivore) based on diet information in the original paper or FishBase (Froese and Pauly 2009). Carbon was excluded from statistical comparisons to avoid problems of multicollinearity and because some studies presented only body N and P contents.

Mean body content across all species was 44.7% C (range 30.2–53.6), 10.1% N (range 6.7–13.2), and 2.9% P (range 1.3–5.7), and interspecific variation showed a unimodal distribution for each element (Figure 2). At both the species and family levels, freshwater fishes varied least in C (coefficient of variation [CV] = 8.3% for species and 7.1% for families), moderately in N (CV = 12.0% and 11.9%), and most in P (CV = 29.8% and 26.4%). Body nutrient ratios showed similar variation among species; molar C:N ranged from 3.8 to 7.7 (mean = 5.2, CV = 13.9%), C:P from 15.9 to 95.9 (mean = 44.0; CV = 33.0%), and N:P from 2.8 to 16.1 (mean = 8.4; CV = 30.0%).

These results make it clear that fish are any-

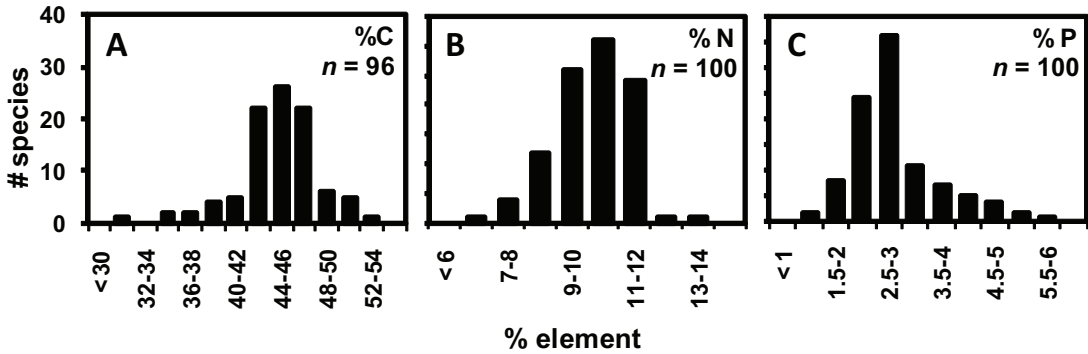


Figure 2. Frequency distributions of body carbon (C) (A), nitrogen (N) (B), and phosphorus (P) (C) content of freshwater fishes in North America, South America, and Europe. Data are from Penczak (1985), Penczak et al. (1985), Sterner and George (2000), Tanner et al. (2000), Vanni et al. (2002), Hendrixson et al. (2007), Dantas and Attayde (2007), and our unpublished work.

thing but homogeneous in their body chemistry. Tropical species covered a much wider range of N and especially P content than temperate species (Figure 3), but preliminary statistical analyses showed no overall difference

between tropical and temperate species after accounting for family affiliation and trophic guild. Together, family and guild assignments explained 74% of the interspecific variation in body N content and 80% for P.

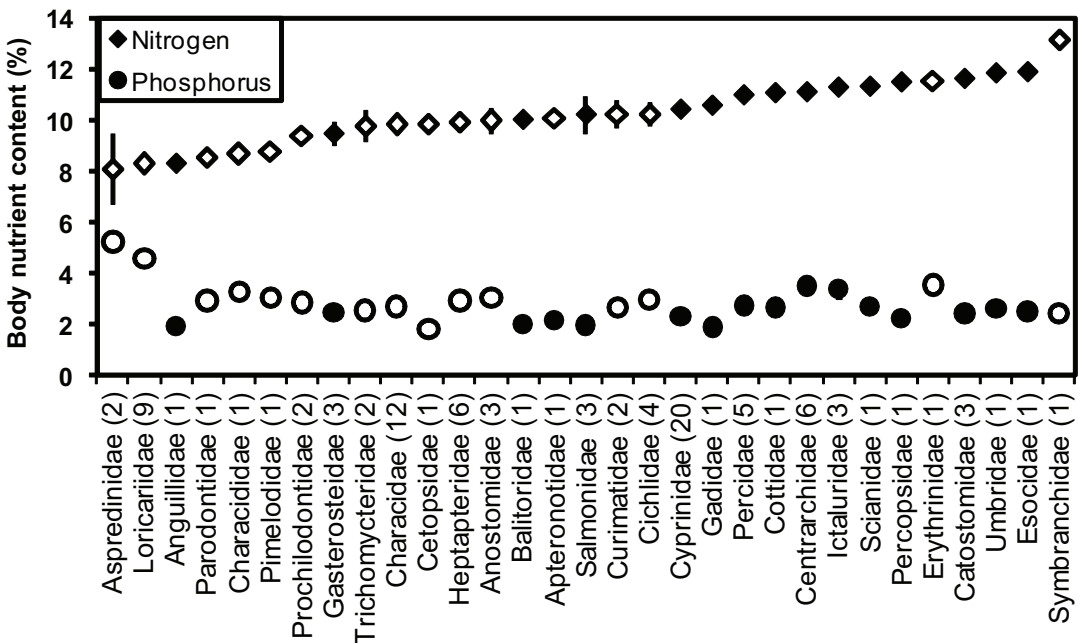


Figure 3. Body nitrogen and phosphorus content by freshwater fish family. Families represented primarily by tropical species are indicated with open symbols; filled symbols denote predominantly temperate species. The number of species per family is indicated in parentheses. Markers indicate means across species; bars indicate 1 SE. Data are from Figure 2.

Multivariate analysis of variance indicated significant differences in body nutrient content among families (Wilks' $\lambda = 0.116$, $F_{60,126} = 4.06$, $P < 0.001$; Figure 3) and trophic guilds (Wilks' $\lambda = 0.685$, $F_{10,126} = 2.62$, $P = 0.006$; Figure 4). Families varied significantly in both N ($F_{30,64} = 3.06$, $P < 0.001$) and P ($F_{30,64} = 4.99$, $P < 0.001$). Pairwise comparisons (Tukey's HSD [honestly significant difference]; $\alpha = 0.05$) indicated that neotropical aspredinid catfish and European anguillid eels had significantly lower body N content than umbrid, symbranchid, ictalurid, and catostomid fishes. Body P differences were dominated by neotropical aspredinid and loricariid catfishes, which had significantly more P than about half the other families. In addition, centrarchids had significantly higher P than salmonids. Guilds differed significantly in N ($F_{5,64} = 3.90$, $P = 0.004$) but not P ($P = 0.194$). Pairwise comparisons indicated that algivores had significantly less body N content than piscivores or generalized carnivores. However, this difference was driven almost entirely by

the low body N content of loricariid catfish, which represented 8 of 10 algivorous species in the data set. No other pairwise comparisons between guilds were significant.

These patterns support some previous conclusions as well as revealing new ones. The high body P of centrarchids relative to minnows or salmonids has long been recognized in studies of North American fishes, and our results confirm that centrarchids are fairly P-rich by temperate standards. However, centrarchids are comparable to many tropical families (e.g., Anostomidae, Cichlidae, and Erythrinidae), and previous generalizations about percids being P-rich were not supported even among temperate fishes (Sterner and George 2000). The neotropical Loricariidae and Aspredinidae emerged as the most P-rich fish families in our survey, which accords with expectations from their anatomy. Loricariids are encased in bony scutes, presumably for defense against predators, whereas aspredinids are known as "banjo catfish" because of their enlarged, dorsolaterally flattened cra-

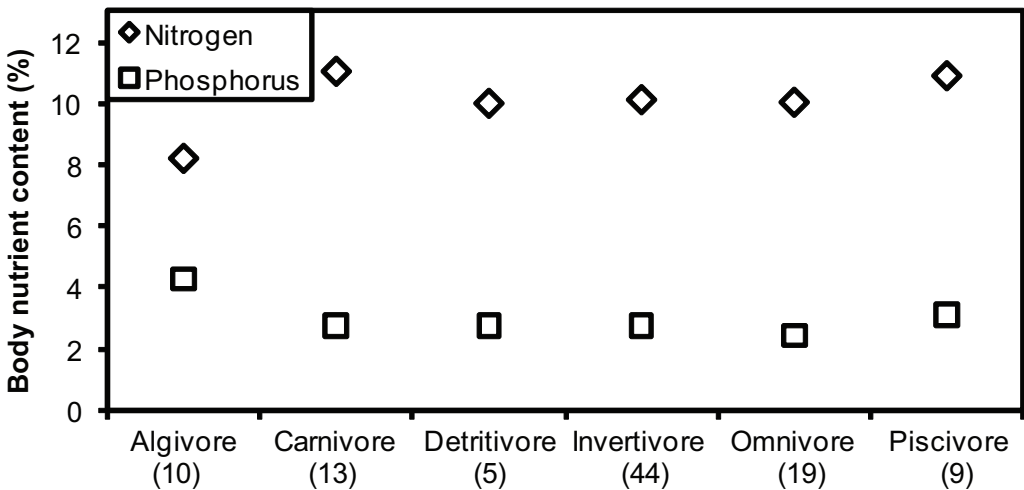


Figure 4. Body nitrogen and phosphorus content by freshwater fish trophic guild. The number of species per guild is indicated in parentheses. The carnivore guild represents generalized predators consuming both fishes and invertebrates, and the omnivore guild represents consumers of both plant and animal material. Markers indicate means across species; bars indicating 1 SE are plotted but are all smaller than the marker. Data are from Figure 2.

nium and pectoral girdles followed by a thin, elongate body.

There was an overall negative correlation between body N and P content across species ($r = -0.31$, $n = 100$, $P = 0.002$) and families ($r = -0.33$, $n = 31$, $P = 0.070$), though both patterns are noisy. This potential relationship could be interpreted as a simple consequence of a zero-sum game of body composition wherein increasing the proportion of body N content must be balanced by a decrease in the proportion of P. However, together N and P summed to a mere 10.0–15.6% of dry mass, suggesting that zero-sum constraints need not be invoked (see also Hendrixson et al. 2007). A more interesting hypothesis is that there exists a trade-off between investment in bone and muscle. For instance, we might speculate that selection favors species that lie on a gradient from a well-armored, sedentary lifestyle (high P, low N) to a flexible, highly mobile lifestyle (low P, high N), such that possessing either high or low values of both N and P would be maladaptive. The same pattern could arise from selection for a gradient in buoyancy, where bony species need not swim as much due to their high body density. Further work will be required to resolve whether there is truly a trade-off between body N and P content. Analyzing variation within a species-rich clade where species share the same general morphology but vary in habitat use, behavior, diet, and other ecological traits would be particularly useful.

So what mechanisms give rise to all this variation in fish body stoichiometry? Recent work has evaluated the influence of body size, phylogenetic affinities, body morphology, and growth rates. Size effects are best assessed within species, thereby controlling for phylogeny and morphology. Intraspecific comparisons within 45 species of temperate and tropical fish indicated that size had no predictable influence in 78% of cases for N and 84% for P (Penczak

1985; Sterner and George 2000; Tanner et al. 2000; Dantas and Attayde 2007; Hendrixson et al. 2007). When size effects were significant, larger individuals had less N in 9 of 10 cases and less P in 4 of 7 cases. Thus, in juvenile and adult freshwater fishes, there is little overall evidence of size effects on body N and P content within species. This lack of pattern contrasts with evidence from terrestrial vertebrates, which must increase their skeletal P investment with mass in order to counter gravitational pull on their bulk (Sterner and Elser 2002). However, there can be substantial shifts in body stoichiometry early in fish ontogeny; larvae of zebrafish and gizzard shad had low body P and high body N content compared to juveniles, giving rise to dramatic shifts in body N:P as young fish began to invest more heavily in skeletal construction (Pilati and Vanni 2007).

Evidence of phylogenetic effects on body stoichiometry of 20 species representing eight families was recently presented by Hendrixson et al. (2007). Their analysis was considerably more sophisticated than the simple family comparisons made in this chapter and elsewhere. They derived a phylogenetic tree indicating the relative evolutionary position of each fish species, then mapped the pattern of body nutrient content and stoichiometric ratios onto the tree. By randomizing the nutrient data across the tree, they demonstrated that there was strong phylogenetic signal in body P, C:P, and N:P, but not in C or N. Subsequent corrections for phylogenetic nonindependence in interspecific comparisons nullified the apparent effects of body size and diet on body nutrient content and stoichiometry in their data set. These results demonstrate the value of phylogenetically explicit analyses of fish nutrient content for disentangling ecological and evolutionary explanations for stoichiometric patterns. It is clear that much exciting work remains to be done in this area.

The overall body shape and growth rate of fish also affects their body stoichiometry. Using the fineness ratio (total length divided by maximum body depth), Tanner et al. (2000) showed that elongate fishes have high body N:P. This contrasts with predictions based on surface area to volume ratios, which would suggest that the greater scale area and length of the spinal column required for an elongate body plan would yield higher P content and lower N:P due to investment in P-rich bone. This conflict may arise in part from the derivation of the fineness ratio, which gives slab-sided fish (e.g., *Lepomis*) low scores though they actually have very high surface area:volume ratios. In any case, recent analyses of body calcium content confirmed that most P in a fish is tied up in bone (Hendrixson et al. 2007; Pilati and Vanni 2007), so skeletal investment remains the most important driver of fish body stoichiometry. Despite the importance of bone, a substantial portion (19–54%) of fish body P content is allocated to other biomolecules, leaving considerable scope for additional influences.

Growth rate is often regarded as the second most important determinant of body N:P after structural demands. Growth requires large amounts of P-rich RNA for transcription and translation, so rapidly growing plants and animals generally have higher P content and lower N:P than slow-growing counterparts (Elser et al. 1996). This pattern has long been recognized by fish biologists in the form of RNA:DNA ratios, which are closely correlated with larval fish growth rates (Buckley 1984; Buckley et al. 2008) but have not been viewed in the context of elemental stoichiometry. However, in contrast to the expected relationship, Tanner et al. (2000) found a strong positive relationship between growth rates and body N:P, suggesting lower P content in fast-growing species. They speculated that this pattern could reflect more rapid growth of N-rich muscle than P-

rich scales and bones, but unfortunately their analyses confounded fish size and growth rate due to use of absolute growth rate (millimeters growth per day) rather than proportional rates (percentage growth per day). This is problematic because small fish are likely to have relatively low absolute growth rates despite high proportional growth rates (and the reverse for large fish). Thus, the low N:P of Tanner et al.'s (2000) slow-growing species might arise simply from the way in which growth rates were expressed. Ontogenetic shifts also must be taken into account. For instance, increases in body P content suggest that investments in bony structures (which increase from larvae to adults) rather than proportional growth rates (which decrease with size) are the primary determinant of body P (Pilati and Vanni 2007). Overall, it remains to be seen whether growth rate variation within or among fish species is indeed sufficient to systematically affect body stoichiometry. Linking body N:P with classic patterns of RNA:DNA ratios in growing fishes seems especially promising.

Finally, we return to the question of homeostasis: do fish really regulate their body nutrient content in a homeostatic way? In parallel to examining variation among species, it is important to empirically evaluate the evidence for homeostatic regulation of body nutrient content within species. We did not undertake our own analysis of homeostasis because the required data on individual fish are rarely presented in the literature, but previous reports are equivocal. Hendrixson et al. (2007) found that bluegills *Lepomis macrochirus* from 12 sites varied in P content by about 1%, after controlling for size. Given that the total range across 100 freshwater fish species is less than 4%, this constitutes considerable intraspecific variation. However, earlier studies found more limited spatial differences among several minnow species (0.4% P, 1.0% N; Sterner and

George 2000) and largemouth bass *Micropterus salmoides* (0.7% P, 0.7% N; Goodyear and Boyd 1972). Overall, it is clear that the body stoichiometry of freshwater fish is regulated, but imperfectly. We now turn to fish diets and how stoichiometric variation among potential prey items compares to that of fish.

Dietary Stoichiometry of Stream Fishes

Collectively, stream fishes can utilize almost every type of organic matter in freshwaters. Detritus and algae are the most abundant resources and are the main diet of many tropical stream fishes and a smaller number of temperate species (Lowe-McConnell 1987; Matthews 1998; Ibanez et al. 2009). Invertebrate animals are major diet items across all latitudes, as are fish. Terrestrial vegetation, including seeds, fruits, flowers, and leaves, is consumed by both generalist and specialist species, particularly in the tropics. In addition to these major categories of diet items, a modest number of stream fishes have evolved unusual trophic specializations, such as consuming wood (e.g., *Panaque*) or the scales (e.g., *Roeboides*), fins (e.g., many piranhas), blood and mucus (e.g., trichomycterid catfishes), or eyes (e.g., cutlips minnow *Exoglossum maxillingua*) of other fishes. Given this range of possible diets, it is important to consider the nutritional implications of alternative trophic strategies. Bioenergetics has often been the focus of such research, but the implications for nutrient acquisition are equally profound.

Due to the variety of food types used by stream fishes, the stoichiometry of their diets varies widely. Traditionally, examinations of diet quality from a nutrient perspective have focused on N, often using protein content as an index. The energy:protein ratio varies predictably among food types, ranging from low

in detritus, terrestrial vegetation, and macrophytes to high in invertebrates and fish (Bowen et al. 1995). Algae occupy an intermediate position in the spectrum, but a substantial range exists within each of these food classes. A focus on caloric and protein content remains prevalent in much research on diet design for pisciculture.

Profiles of the elemental stoichiometry of alternative diet items have borne out the generalization that diet quality increases from terrestrial plants to detritus to algae to invertebrates to fish. However, accounting for even three elements (C, N, and P) reveals that nutritional ecology of stream fishes is more complicated and interesting than previously realized. Several recent studies have summarized the C:N:P stoichiometry of benthic invertebrates and other food resources (Cross et al. 2005; Evans-White et al. 2005; Liess and Hillebrand 2005). The N and P content of all possible diet items except bacteria is less than that of fishes themselves (Figure 5; Cross et al. 2005). Thus, only consumption of other fish or of bacteria would support a truly stoichiometrically balanced diet for a fish. Invertebrates, particularly predatory species, are close to fishes in N content, but their median C:P ratio is roughly four-fold higher than that of fishes.

Detritivorous, algivorous, herbivorous, and frugivorous stream fishes face the greatest nutritional challenges. Their diets have C:N ratios that are 5–75 times higher than their needs for growth, and C:P ratios that are one to two orders of magnitude higher (Figure 5). In addition, the caloric value of carbon biomolecules in plant-based foods is substantially lower than that provided by a carnivorous diet (Bowen et al. 1995). Thus, feeding as a primary consumer requires subsistence on a diet that is both nutrient-poor and energy-poor. In addition, plant material is often challenging to digest, requiring anatomical and physi-

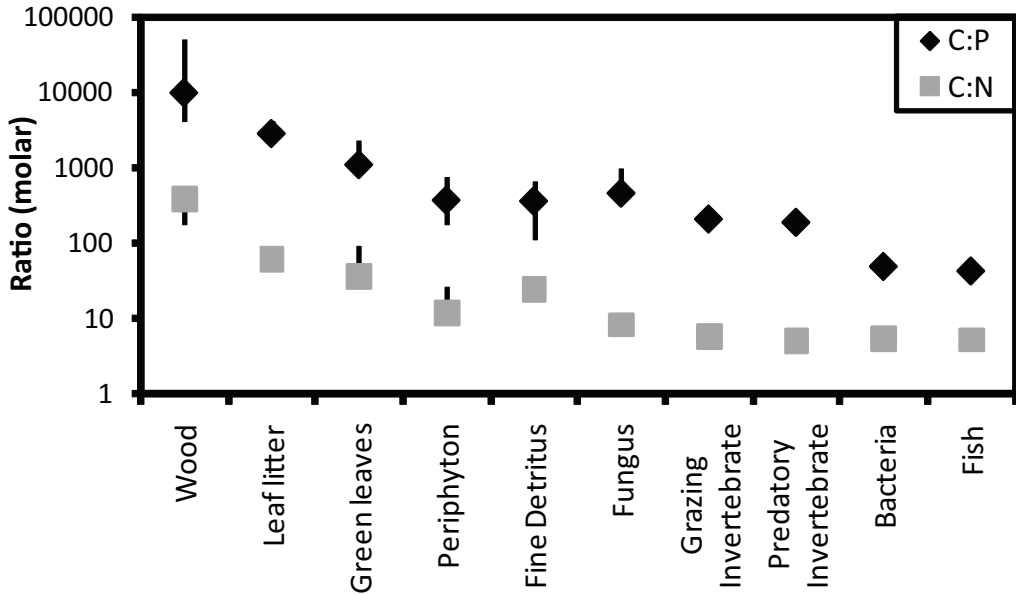


Figure 5. Carbon:nutrient stoichiometry of diet items of stream fishes. Note the \log_{10} scale of the y-axis. Markers indicate median of measurements reported in the literature; bars indicate 25th and 75th percentiles. Food source data are from Cross et al. (2005); fish data are from Figure 2.

ological specializations (Choat and Clements 1998). To compensate for the low nutritional quality of plant and detrital material, primary consumer fishes eat larger quantities of food than carnivorous counterparts (e.g., Grimm 1988). Our summary of body nutrient content data for algivores suggests that they may also have minimal N demands to support growth (Figure 4), though this pattern was driven by results from neotropical armoured catfishes and may not be generalizable. Body P content of algivores and detritivores is at least as high as that of fishes feeding on more P-rich prey, highlighting the stoichiometric imbalance they must overcome.

A stoichiometric perspective also informs perspectives on foraging by invertivorous stream fishes. Stream invertebrates representing three phyla and seven orders are all P-poor compared to the fishes that consume them; differences range from 2- to 26-fold, but the imbalance depends primarily on the identity of

the fish rather than the invertebrate (Figure 6). In addition, invertebrate species vary almost two-fold in their N content, and there are systematic differences among taxa. For instance, crustaceans are uniformly low in N, whereas predatory odonates and megaloptera are substantially richer in N (Figure 6; Evans-White et al. 2005). Thus, fishes that target predatory insects or certain snail species can obtain greater dietary N than counterparts that feed upon similar biomass of amphipods, isopods, or crayfish.

Striking disparities between the nutrient content of fish tissues and fish diets raise the question of whether fish growth could be limited by nutrient assimilation. Carbon:nutrient ratios alone are insufficient to resolve thresholds for nutrient limitation because all animals have metabolic demands for energy that necessitate access to much more C than is reflected in tissue growth or reproductive output (Anderson et al. 2005). Bioenergetics models have

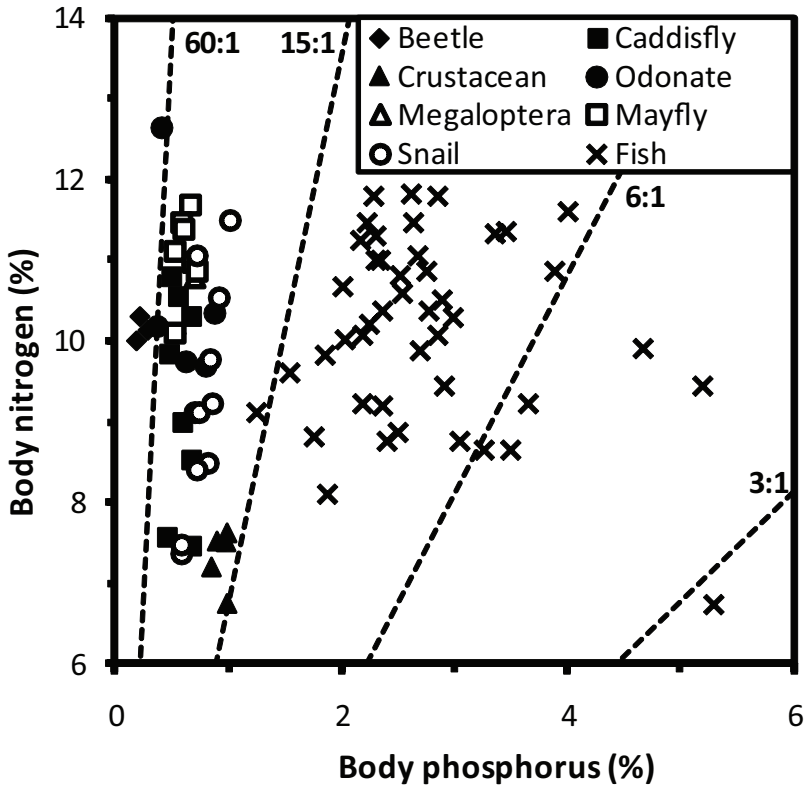


Figure 6. Nitrogen and phosphorus content of stream invertebrates and invertivorous fishes. Markers indicate mean values for one species based on whole-body analyses. Invertebrate data are from Evans-White et al. (2005), and fish data represent only the invertivorous species from Figure 2. Dashed lines represent isopleths of molar N:P ratios, as marked.

been coupled with stoichiometric models to evaluate whether fish growth is more likely to be limited by energy or nutrients, with an emphasis on P because dietary N:P exceeds body N:P for all fishes but piscivores. Schindler and Eby (1997) compared growth rates observed in nature to those expected under P limitation for 18 carnivorous fish species and concluded that P limitation of fish growth occurs rarely if ever. Frost et al. (2006) calculated threshold dietary C:P ratios above which growth would be limited by P for nine freshwater and marine fish species, finding a range of 77–197. Interestingly, two of the three species with a threshold C:P of less than 110 are largely herbivorous (82 in tilapia *Oreochromis* sp.; 107

in roach *Rutilus rutilus*), yet periphyton C:P is greater than 178 in 75% of reported data (Cross et al. 2005) and C:P of aquatic macrophytes and terrestrial vegetation is considerably higher. Thus, it appears that herbivorous and detritivorous stream fishes are certain to be near the boundary between energy and P limitation of growth. Only one indirect test of this hypothesis has been conducted, using two species of armored catfish from Neotropical rivers whose bony scutes give them some of the highest body P contents recorded from fishes (Loricariidae in Figure 3). Hood et al. (2005) found that growth of both species was almost certainly P limited due to their P-poor diet of periphyton.

The combination of theoretical and empirical evidence for P limitation of growth in primary consumer fishes is intriguing, but energy limitation of growth rates remains the prevailing paradigm in fish nutritional ecology. Comparing the modeled threshold element ratios for carnivorous fishes to dietary stoichiometry of invertebrates suggests that nutrient limitation should be reconsidered, even for some carnivores. Carnivorous species show a broad range of threshold dietary C:P ratios (77–197; Frost et al. 2006), but a large majority of stream mayfly, caddisfly, odonate, and beetle species have even higher C:P ratios (Figure 6; Evans-White et al. 2005). Thus, it is plausible that even insectivorous stream fishes, which dominate fish assemblages in many temperate and tropical streams, are sometimes P limited in their growth. Indeed, energy limitation appears to be a certainty only in piscivores, whose diet is by definition in stoichiometric balance with their growth requirements for N and P. These uncertainties beg for further refinement of coupled bioenergetics and stoichiometric models for application of fish and other nutrient-rich consumers. Developing such models in concert with field-based assessments of natural variation in body and dietary stoichiometry will be particularly useful. Nonetheless, we are now ready to consider the fate of excess dietary nutrients that are not incorporated into body tissues, but rather recycled back into stream ecosystems.

Role of Fishes in Stream Nutrient Cycling

Ingested nutrients that are not incorporated into a fish's body tissues must be defecated or excreted. As outlined earlier (Figure 1), nutrient recycling must obey the constraints of mass balance; recycling rates are a positive function of ingestion rates for a given nutrient and a neg-

ative function of the consumer's body content of that nutrient. In light of the great variation in nutrient content of both the body tissues and the diet of stream fishes, we would predict an equally broad range in nutrient recycling rates and ratios (Figure 1).

Overlaid upon these sources of variation is the efficiency with which fish can assimilate nutrients from their diet. It has long been recognized that assimilation efficiencies are low for primary consumers and high for carnivores (Welch 1968; Sterner and Hessen 1994). For instance, loricariid catfish only assimilate about half of their dietary N and P (Hood et al. 2005). The figure is roughly 40% for tilapia in African lakes (Tadesse 1999) but more than 70% for some marine (Sturm and Horn 1998) and temperate stream algivores (Grimm 1988). Thus, nutrient recycling rates for primary consumers may be low due to both scarcity of nutrients in their diet and low efficiency of extracting those nutrients, leaving little surplus after meeting nutrient demands for growth and reproduction. Nonetheless, Hood et al. (2005) found that armored catfish continued to excrete small amounts of P, even when mass-balance budgets suggested that there should be no surplus P to recycle. This result supports the contention that basal metabolism requires some minimal recycling of nutrients even when dietary nutrients are scarce (Anderson and Hessen 2005), though the issue remains poorly understood.

Recycled nutrients are released in both dissolved and particulate forms. Fish feces contain around half of recycled nutrients (e.g., Grimm 1988; Andre et al. 2003), and the particulate recycling pathway has several distinctive properties. First, feces may exhibit lower N:P than dissolved wastes, due to retention of P in solid wastes such as bones and sediment. Second, they sink rapidly, thereby concentrating the remineralization process on the bottom. Final-

ly, feces require additional processing by microbes in order to release all nutrients, so their contribution to available nutrient pools occurs considerably later than excretion of dissolved N and P. Despite broad interest in detrital processing in streams, the magnitude and fate of fecal nutrients released by fishes has received little attention.

Most of the dissolved N and P excreted by freshwater fish is in chemical forms— NH_4^+ and soluble reactive phosphorus, respectively—that are readily available to primary producers and microbes. In this way, excretion provides a rapid recycling pathway that transforms nutrients stored in prey into dissolved compounds that can fuel further primary production or decomposition. In nutrient-poor systems, nutrient recycling fluxes from fishes can contribute much more to ecosystem functioning than would be inferred from energy flow (Grimm 1988; McIntyre et al. 2007). Along with these readily available N and P compounds, nutrients can also be excreted as dissolved organic compounds that require microbial processing before becoming bioavailable (Anderson et al. 2005).

Surveys of nutrient excretion by freshwater fishes have revealed extensive variation among species, as expected from ecological stoichiometry theory. Most of this research has been conducted in lakes (Hall et al. 2007), but our work on the diverse fish fauna of Rio Las Marias, Venezuela also has yielded many insights into nutrient excretion dynamics. The most fundamental pattern emerging from research in lotic, lentic, and marine ecosystems is strong scaling of excretion rates with body size. Hall et al. (2007) reviewed the available data from 30 fish species and concluded that positive or negative allometric scaling was evident in some individual species but that cross-species patterns indicate direct proportionality of excretion rates of N and P with size. Analy-

ses of 47 species from Rio Las Marias strongly support the overall importance of body size (Figure 7). However, we found that species vary most widely in the size-scaling of P excretion and that P excretion increases more slowly with size than N excretion across spe-

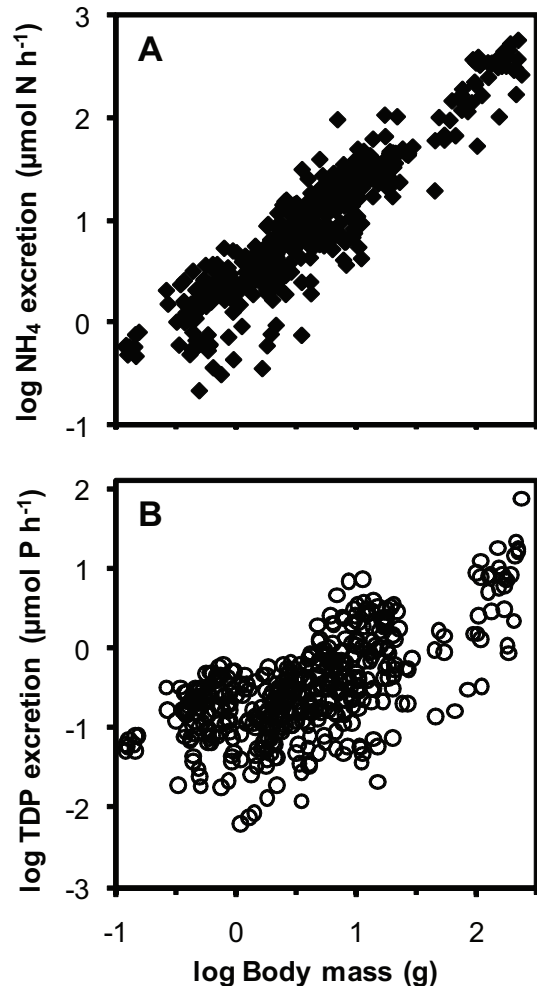


Figure 7. Size-scaling of nitrogen (A) and phosphorus (B) excretion rates in Rio Las Marias, Venezuela. Markers represent measurements from 449 separate incubations involving 47 different fish species. N excretion was measured as $\text{NH}_4\text{-N}$; P excretion was measured as total dissolved P (TDP). Note the steeper scaling of N excretion than P excretion. Data are from McIntyre et al. (2008).

cies (Vanni et al. 2002; McIntyre et al. 2008). As a result, the N:P ratio of excreted nutrients increased substantially with body size; on average, large fishes excreted relatively more N than P compared to smaller counterparts.

Phylogenetic influences are also evident in the Rio Las Marias data set. Vanni et al. (2002) showed that the high body P of loricariid catfishes leads to low P excretion rates in both algivorous and carnivorous species, and inclusion of additional species supported this finding (McIntyre et al. 2008). At the other end of the spectrum, minnow-like tetras have consistently low body P and excrete at relatively low N:P ratios regardless of diet. Comparing body N:P to excreted N:P across dozens of species confirms that body stoichiometry is the likely driver of excretion stoichiometry in this ecosystem, particularly when very-low-P tadpoles are included in the comparisons (Vanni et al. 2002). However, formal tests of phylogenetic signal in excretion rates and ratios have yet to be conducted.

Regardless of its mechanistic basis, the large differences among species in nutrient recycling rates and excreted N:P offer a compelling way to link species identity and biodiversity with the functioning of stream ecosystems. For instance, rates of N and P excretion vary among fish species in Rio Las Marias by several orders of magnitude, yielding 10-fold differences in excreted N:P (Figure 8). This has profound implications for nutrient cycling. For instance, patterns in the size-structure and species composition of fish assemblages yield average aggregate P excretion rates that are twice as high in riffles as in runs, yet aggregate N excretion rates that are comparable between habitats. Indeed, the heterogeneous distribution of fish biomass and individual species along the length of the river creates more than 10-fold variation in aggregate excretion rates of either N or P per unit area (McIntyre et al. 2008). When these patterns are considered from the standpoint of fish extinctions in Rio Las Marias, interspecific differences in body and excretion stoichiometry could give rise to

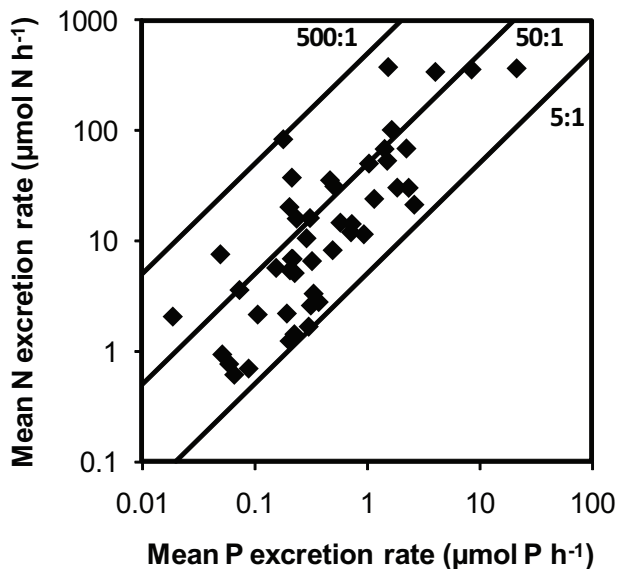


Figure 8. Stoichiometry of nutrient excretion by fishes in Rio Las Marias, Venezuela. Markers indicate mean excretion rates of N and P for each of 47 species. Lines indicate isopleths of excreted N:P molar ratios, as indicated. Data are from McIntyre et al. (2008).

dramatic swings in aggregate excreted N:P as a function of the order in which species are lost (McIntyre et al. 2007).

Nutrient recycling by fishes can be a quantitatively important flux in many freshwater ecosystems (Vanni 2002). Recycling of dissolved nutrients by stream fishes was first placed in an ecosystem context by Grimm (1988), who concluded that N excretion by longfin dace *Agosia chrysogaster* in Sycamore Creek, Arizona represents 5–10% of ecosystem N demand. In Rio Las Marias, aggregate N excretion by the entire fish assemblage was equivalent to roughly 75% of dissolved inorganic N uptake (Vanni et al. 2002; McIntyre et al. 2008). However, enormous differences in fish biomass and assemblage composition among individual riffles and runs led to a range of 9–415% of N uptake that could be supplied by fish excretion. In contrast to the importance of fishes in N cycling in Rio Las Marias, excretion of P by this diverse assemblage was trivial relative to ambient P supplied by weathering of minerals upstream (McIntyre et al. 2008).

The importance of N recycling by fishes in Sycamore Creek and Rio Las Marias is impressive but not altogether unexpected. Primary producers in both ecosystems are strongly N-limited; therefore, any substantial recycling flux could influence ecosystem functioning. Common sense and experimental results indicate that nutrient recycling by animals is most important in nutrient-starved ecosystems (Evans-White and Lamberti 2006) where it can represent a large proportion of total nutrient fluxes compared to nutrient-replete ecosystems. In addition, the stoichiometric imbalance between most fishes and their prey is more extreme for P than for N (e.g., Figure 6), leading to higher retention of dietary P than N. As a result, fishes are likely to recycle nutrients at high N:P ratios, hence contributing more to recycling of N than P (Figure 1).

Though direct impacts of excreted nutrients are difficult to demonstrate in real streams and rivers, results from mesocosm experiments are strongly suggestive. Invertebrate grazers in lakes (e.g., Urabe et al. 2002; Liess et al. 2006) and streams (Evans-White and Lamberti 2005) generally enhance dissolved nutrient concentrations and algal nutrient content. Experiments comparing the effects of stream grazers that differ in body stoichiometry support the predicted causal chain from consumer body N:P to recycling N:P to dissolved N:P to periphyton N:P (Evans-White and Lamberti 2005; Knoll et al. 2009). For instance, armored catfish (low body N:P) and tadpoles (high body N:P) from Rio Las Marias drive periphyton N:P in opposite directions, and a ^{15}N tracer proved that this effect is mediated by greater N recycling by the fish (Knoll et al. 2009). Collectively, these experiments under simplified conditions strongly support the potential for stoichiometric feedbacks from the identity of consumers to the quality of food resources, particular for primary consumers.

This concept is currently being extended into the realm of evolutionary biology through studies of nutrient recycling by guppies in Trinidadian streams. Guppies from high-predation streams consistently excrete N and P at higher rates than counterparts from low-predation streams, potentially contributing to faster algal accrual (Palkovacs et al. 2009). This result shows that seemingly unrelated evolutionary pressures on stream fish phenotypes can have important consequences for nutrient recycling, thereby creating a mechanistic link between the dynamics of evolutionary interactions and ecosystem functioning.

In addition to recycling dietary nutrients, mortality of fishes in streams can provide a critical source of nutrients as their body tissues degrade, particularly in the case of migratory species (see Flecker et al. 2010, this volume).

Pacific salmon are the most celebrated example due to their huge migrations and semelparous life history. Salmon carcasses fertilize spawning streams, enhancing primary and secondary productivity (Schindler et al. 2003). Similar effects arise from mortality of alewife *Alosa pseudoharengus* (Durbin et al. 1979) and probably many other anadromous fishes. These inputs have not yet been placed in a stoichiometric framework to examine their characteristic N:P and whether migratory fishes could shift a stream from N-limitation to P-limitation or the reverse. Nutrient excretion by live Pacific salmon (Janetski et al. 2009) and alewife (Post and Walters 2009) can also provide an important source of nutrients to stream ecosystems that is independent of spawner mortality. The relative importance of excretion versus mortality for nutrient cycling in streams receiving fish migrations will depend on mortality rates, run size, and ecosystem nutrient status (Flecker et al. 2010).

Conclusions

Ecological stoichiometry provides a conceptual framework for unifying many aspects of stream fish physiology, population ecology, community interactions, ecosystem roles, and evolutionary biology. Our review of patterns in body, dietary, and recycling stoichiometry reveals remarkable progress over the past two decades in documenting stoichiometric patterns in nature and elucidating their underpinnings. However, many theoretical predictions remain to be tested and only a modest portion of stream fish diversity has yet been analyzed from a stoichiometric perspective. Moreover, despite successful efforts to characterize stoichiometric variation in fishes themselves, diet items, and excreted wastes, the full connections among these three major terms in the mass-balance equation for fish

nutrient dynamics still await rigorous quantitative assessment.

Before closing, we must also point out the great potential that exists for integrating ecological stoichiometry with traditional interdisciplinary perspectives on fish ecology. For instance, fisheries biologists rarely think of managing fish catches in terms of nutrients, yet harvesting fish can in fact constitute a major term in ecosystem nutrient budgets (Maranger et al. 2008), for better or worse. At the other end of the spectrum, bioenergetics modeling has revolutionized understanding of the physiological and nutritional constraints on individual fish (Hartman and Kitchell 2008) but has rarely been brought to bear on questions in ecological stoichiometry of fishes. A few attempts in that vein have yielded intriguing patterns (Schindler and Eby 1997; Hood et al. 2005), and bioenergetics approaches have been very fruitful with zooplankton (e.g., Anderson et al. 2005). Further efforts to merge bioenergetics modeling with field data on the diversity of body and dietary stoichiometry in fishes will surely be informative. More specifically, aquaculture continues to spur research on the role of nutrients in fish nutrition, yet the analyses of energy (C), protein (N), and bone (P) content so often applied to prepared diets are almost never framed in terms of C:N:P stoichiometry. Such a conceptual merger could allow the translation of basic research results into practical benefits for captive production of food fish, as well as tapping a huge body of nutritional work for new stoichiometric insights. These are just a few examples of how research on ecological stoichiometry could be joined with more conventional approaches to fish ecology.

It will be exciting to see what insights will emerge from additional field data, further experimentation, and greater integration of ecological stoichiometry into theoretical models

of organismal and ecosystem ecology. We anticipate particularly important opportunities in the following five areas: (1) assessing whether fishes and other consumers act as optimal foragers when nutrients are evaluated alongside energetic considerations; (2) analyzing the evolutionary conservatism of body and excretion stoichiometry, and associated constraints on diet and roles in ecosystem functioning; (3) merging the spatial ecology of animals and nutrients to understand the conditions under which consumers respond to versus drive nutrient availability; (4) combining stoichiometric and food web linkage data to generate trophochemical webs (Sterner et al. 1996) that elucidate how consumer community structure affects biogeochemistry through nutrient storage and recycling; and (5) including elements other than C, N, and P in stoichiometric analyses to explore the importance of micronutrients and trace elements. These issues and the many stimulating suggestions provided by Sterner and Elser (2002) will offer fodder for decades of fruitful research on ecological stoichiometry in aquatic ecosystems. The resulting integration of perspectives across individual, population, community, and ecosystem levels promises great insight into the ecology of stream fishes.

Acknowledgments

We thank Don Jackson and Keith Gido for organizing the symposium and spurring us to think more deeply about ecological stoichiometry and stream fishes. Our thinking has also been sharpened by discussions with Mike Vanni, Jim Hood, Daniel Schindler, Yvonne Vadeboncoeur, and J. David Allan. Insightful comments from two anonymous reviewers improved the manuscript. Our research was made possible by support from the David H. Smith Conservation Research Fellowship (PBM) and NSF grants INT-0321443, DEB-0321471, DEB-0319593, and DEB 0841822.

References

- Anderson, T. R., and D. O. Hessen. 2005. Threshold elemental ratios for carbon versus phosphorus limitation in *Daphnia*. *Freshwater Biology* 50:2063–2075.
- Anderson, T. R., D. O. Hessen, J.J. Elser, and J. Urabe. 2005. Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. *American Naturalist* 165:1–15.
- Andre, E. R., R. E. Hecky, and H. C. Duthie. 2003. Nitrogen and phosphorus regeneration by cichlids in the littoral zone of Lake Malawi, Africa. *Journal of Great Lakes Research* 29S 2:190–201.
- Bowen, S. H., E. V. Lutz, and M. O. Ahlgren. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology* 76:899–907.
- Buckley, L. J. 1984. RNA-DNA ratio: an index of larval fish growth in the sea. *Marine Biology* 80:291–298.
- Buckley, L. J., E. M. Calderone, and C. Clemmesen. 2008. Multi-species larval fish growth model based on temperature and fluorometrically derived RNA/DNA ratios: results from a meta-analysis. *Marine Ecology Progress Series* 371:221–232.
- Choat, J. H., and K. D. Clements. 1998. Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. *Annual Review of Ecology and Systematics* 29:375–403.
- Cotner, J. B., W. Makino, and B. A. Biddanda. 2006. Temperature affects stoichiometry and biochemical composition of *Escherichia coli*. *Microbial Ecology* 52:26–33.
- Cross, W. F., J. P. Benstead, P.C. Frost, and S. A. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. *Freshwater Biology* 50:1895–1912.
- Dantas, M. C., and J. L. Attayde. 2007. Nitrogen and phosphorus content of some temperate and tropical freshwater fishes. *Journal of Fish Biology* 70:100–108.
- Davis, J. A., and C. E. Boyd. 1978. Concentrations of selected elements and ash in bluegill (*Lepomis macrochirus*) and certain other freshwater fish. *Transactions of the American Fisheries Society* 107:862–867.
- Dodds, W. K. 2007. Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology and Evolution* 22:669–676.
- Durbin, A. G., S. W. Nixon, and C. O. Oviatt. 1979. Effects of the spawning migration of the alewife,

- Alosa pseudoharengus*, on freshwater ecosystems. *Ecology* 60:8–17.
- Elser, J. J., D. R. Dobberfuhl, N.A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry: toward a unified view of cellular and ecosystem processes. *BioScience* 46:674–684.
- Elser, J. J., M. M. Elser, N.A. MacKay, and S. R. Carpenter. 1988. Zooplankton-mediated transitions between N and P limited algal growth. *Limnology and Oceanography* 33:1–14.
- Evans-White, M. A., and G. A. Lamberti. 2006. Stoichiometry of consumer-driven nutrient recycling across nutrient regimes in streams. *Ecology Letters* 9:1186–1197.
- Evans-White, M. A., and G. A. Lamberti. 2005. Grazer species effects on epilithon nutrient composition. *Freshwater Biology* 50:1853–1863.
- Evans-White, M. A., R. S. Stelzer, and G. A. Lamberti. 2005. Regional and taxonomic patterns in benthic macroinvertebrate elemental composition in streams. *Freshwater Biology* 50:1786–1799.
- Flecker, A. S., P. B. McIntyre, J. W. Moore, J. T. Anderson, B. W. Taylor, and R. O. Hall, Jr. 2010. Migratory fishes as material and process subsidies in riverine ecosystems. Pages 559–592 in K. B. Gido and D. Jackson, editors. *Community ecology of stream fishes: concepts, approaches, and techniques*. American Fisheries Society, Symposium 73, Bethesda, Maryland.
- Froese, R., and D. Pauly, editors. 2009. FishBase. Available: www.fishbase.org (July 2009).
- Frost, P. C., J. P. Benstead, W. F. Cross, H. Hillebrand, J. H. Larson, M. A. Xenopoulos, and T. Yoshida. 2006. Threshold elemental ratios of carbon and phosphorus in aquatic consumers. *Ecology Letters* 9:774–779.
- Goodyear, C. P., and C. E. Boyd. 1972. Elemental composition of largemouth bass. *Transactions of the American Fisheries Society* 101:545–547.
- Griffiths, D. 2006. The direct contribution of fish to lake phosphorus cycles. *Ecology of Freshwater Fish* 15:86–95.
- Grimm, N. B. 1988. Feeding dynamics, nitrogen budgets, and ecosystem role of a desert stream omnivore, *Agosia chryso-gaster* (Pisces: Cyprinidae). *Environmental Biology of Fishes* 21:143–152.
- Hall, R.O., B.J. Koch, M.C. Marshall, B.W. Taylor, and L.M. Tronstad. 2007. How body size mediates the role of animals in nutrient cycling in aquatic ecosystems. Pages 286–305 in A. Hildrew, D. Raffaelli, and R. Edmonds-Brown, editors. *Body size: the structure and function of aquatic ecosystems*. Cambridge University Press, Cambridge, UK.
- Hartman, K. J., and J. F. Kitchell. 2008. Bioenergetics modeling progress since the 1992 symposium. *Transactions of the American Fisheries Society* 137:216–223.
- Hendrixson, H. A., R. W. Sterner, and A. D. Kay. 2007. Elemental stoichiometry of freshwater fishes in relation to phylogeny, allometry and ecology. *Journal of Fish Biology* 70:121–140.
- Hood, J. M., M. J. Vanni, and A. S. Flecker. 2005. Nutrient recycling by two phosphorus-rich grazing catfish: potential for phosphorus limitation of fish growth. *Oecologia* 146:247–257.
- Ibanez, C., J. Belliard, R. M. Hughes, P. Irz, A. Kamdem-Toham, N. Lamouroux, P. A. Tedesco, and T. Oberdorff. 2009. Convergence of temperate and tropical stream fish assemblages. *Ecography* 32:658–670.
- Janetski, D., D. T. Chaloner, S.D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon in stream ecosystems: a quantitative synthesis. *Oecologia* 158:583–95.
- Klausmeier, C. A., E. Litchman, T. Daufresne, and S. A. Levin. 2004. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature (London)* 429:171–174.
- Knoll, L., P. B. McIntyre, M.J. Vanni, and A. S. Flecker. 2009. Feedbacks of consumer nutrient recycling on producer biomass and stoichiometry: separating direct and indirect effects. *Oikos* 118:1732–1742.
- Liess, A., and H. Hillebrand. 2005. Stoichiometric variation in C:N, C:P, and N:P ratios of littoral benthic invertebrates. *Journal of the North American Benthological Society* 24:256–269.
- Liess, A., J. Olsson, M. Quevedo, P. Eklov, T. Vrede, and H. Hillebrand. 2006. Food web complexity affects stoichiometric and trophic interactions. *Oikos* 114:117–125.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore, Maryland.
- Lowe-McConnell, R. H. 1987. *Ecological studies in tropical fish communities*. Cambridge University Press, Cambridge, UK.
- Maranger, R., N. Caraco, J. Duhamel, and M. Amyot. 2008. Nitrogen transfer from sea to land via commercial fisheries. *Nature Geoscience* 1:111–112.
- Matthews, W. J. 1998. *Patterns in freshwater fish ecology*. Chapman and Hall, New York.
- McIntyre, P. B., A. S. Flecker, M. J. Vanni, J. Hood, B.

- W. Taylor, and S. A. Thomas. 2008. Fish distributions and nutrient recycling in a tropical stream: can fish create biogeochemical hotspots? *Ecology* 89:2335–2346.
- McIntyre, P. B., L. Jones, A. S. Flecker, and M. J. Vanni. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. *Proceedings of the National Academy of Sciences of the United States of America* 104:4461–4466.
- Palkovacs, E. P., M. C. Marshall, B. A. Lamphere, B. R. Lynch, D. J. Weese, D. F. Fraser, D. N. Reznick, C. M. Pringle, and M. T. Kinnison. 2009. Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philosophical Transactions of the Royal Society B* 364:1617–1628.
- Penczak, T. 1985. Phosphorus, nitrogen, and carbon cycling of fish populations in two lowland rivers in Poland. *Hydrobiologia* 120:159–165.
- Penczak, T., M. Molinski, W. Galicka, and A. Prejs. 1985. Factors affecting nutrient budget in lakes of the R. Jorka watershed (Masurian lakeland, Poland) VII. Input and removal of nutrients with fish. *Ekologia Polska* 33:301–309.
- Pilati, A., and M. J. Vanni. 2007. Ontogeny, diet shifts, and nutrient stoichiometry in fish. *Oikos* 116:1663–1674.
- Post, D. M., and A. W. Walters. 2009. Nutrient excretion rates of anadromous alewives during their spawning migration. *Transactions of the American Fisheries Society* 138:264–268.
- Redfield, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46:205–221.
- Reiners, W. A. 1986. Complementary models for ecosystems. *American Naturalist* 127:59–73.
- Schindler, D. E., and L. A. Eby. 1997. Stoichiometry of fishes and their prey: implications for nutrient recycling. *Ecology* 78:1816–1831.
- Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* 1:31–37.
- Sterner, R. W., J. J. Elser, T. H. Chrzanowski, J. H. Schampel, and N. B. George. 1996. Biogeochemistry and trophic ecology: a new food web diagram. Pages 72–80 in G. A. Polis and K. O. Wine-miller, editors. *Food webs: integration of pattern and process*. Chapman and Hall, New York.
- Sterner, R. W., and D. O. Hessen. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology and Systematics* 25:1–29.
- Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey.
- Sterner, R. W., and N. B. George. 2000. Carbon, nitrogen and phosphorus stoichiometry of cyprinid fishes. *Ecology* 81:127–140.
- Sturm, E. A., and M. H. Horn. 1998. Food habits, gut morphology and pH, and assimilation efficiency of the zebraperch *Hermosilla azurea*, an herbivorous kyphosid fish of temperate marine waters. *Marine Biology* 132:515–522.
- Tadesse, Z. 1999. The nutritional status and digestibility of *Oreochromis niloticus* L. diet in Lake Langeno, Ethiopia. *Hydrobiologia* 416:97–106.
- Tanner, D. K., J. C. Brazner, and V. J. Brady. 2000. Factors influencing carbon, nitrogen, and phosphorus content of fish from a Lake Superior coastal wetland. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1243–1251.
- Urabe, J., J. J. Elser, M. Kyle, T. Yoshida, T. Sekino, and Z. Kawabata. 2002. Herbivorous animals can mitigate unfavourable ratios of energy and material supplies by enhancing nutrient recycling. *Ecology Letters* 5:177–185.
- Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* 33:341–370.
- Vanni, M. J., A. S. Flecker, J. M. Hood, and J. L. Headworth. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecology Letters* 5:285–293.
- Welch, H. E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. *Ecology* 49:755–759.