

Community connections that link species and support the flow of energy and nutrients between abiotic and biotic spheres of the environment arise from many interactions among organisms. For instance, food webs and energy flow diagrams depict the network of vertical and horizontal linkages extending from basal food resources to top consumers in an integrated visualization of a biological community. Although the number of connecting links can be very large, a modest number of species often make up the majority of the biomass and are responsible for most energy flow. Species also can be grouped together based on their functional similarity in regard to feeding ecology, productivity, capacity for elemental mineralization, etc., revealing their common roles in shaping the structure and function of ecosystems. Some species have complementary or overlapping roles, suggesting that they are functionally redundant for a given function, but at least in some cases certain species appear to be functionally irreplaceable. Thus, the potential loss of a species from communities due to over-harvest, habitat degradation, or other human actions implies that simplified biological communities may be functionally distinct from communities observed in their unaltered state.

In this chapter, we examine some of the ways in which scientists study interactions between aquatic communities and the flow of energy and nutrients. Specifically, we will focus on two concepts that are inextricably linked to one another: food web ecology and the functional role of communities in ecosystem processes.

12.1 Food Web Ecology

Food webs describe the network of consumer-resource interactions among a group of organisms (Layman et al. 2015). The network of interactions depicted in a food web provides one of the most complete, yet succinct, visual summaries of a biological community. The community is

assembled from a regional species pool, as individual species are matched with available resources and habitats, influenced by disturbance and dispersal, and modified by the internal dynamics of species interactions. The study of food webs has a long history in ecology, incorporating at least two major lines of inquiry: one emphasizing how species are inextricably linked through their interactions with one another, hence focusing on population and species interactions as discussed in Chaps. 10 and 11; the other concerned with the flux of organic matter and energy that we will discuss here. Most examples can be categorized very roughly as connectance food webs, which attempt to identify all possible linkages; energy flux food webs, which quantify organic matter flow along a limited number of major pathways; and trophic-interaction food webs, which emphasize population processes and species interactions.

An impressively detailed food web for the Broadstone Stream in southern England provides an excellent example of a connectivity food web (Fig. 12.1). All species are of equal importance in a connectance web and all lines are of equal weight, because the web is constructed from diet presence-absence data. This food web is amongst the most detailed on record and includes all of the benthic community including macrofauna, meiofauna, protozoa, and algae (Schmid-Arroya et al. 2002; Woodward et al. 2005). It includes 131 consumer species supported by eight basal resources and three additional food sources such as eggs, for a total of 842 links. The meiofauna comprise 70% of the species present, demonstrating the need to include small-bodied organisms in this type of analysis. Food web structure varied seasonally due to changes in species richness, resulting in temporal changes in the proportion of species at the top and the base of the food web. Despite its complexity, relatively simple patterns in food web structure could be found in relation to body size. Meiofaunal and macrofaunal sub-webs were effectively two compartments because large prey were invulnerable to small predators and large predators were not effective in consuming very small prey (Woodward et al. 2005).

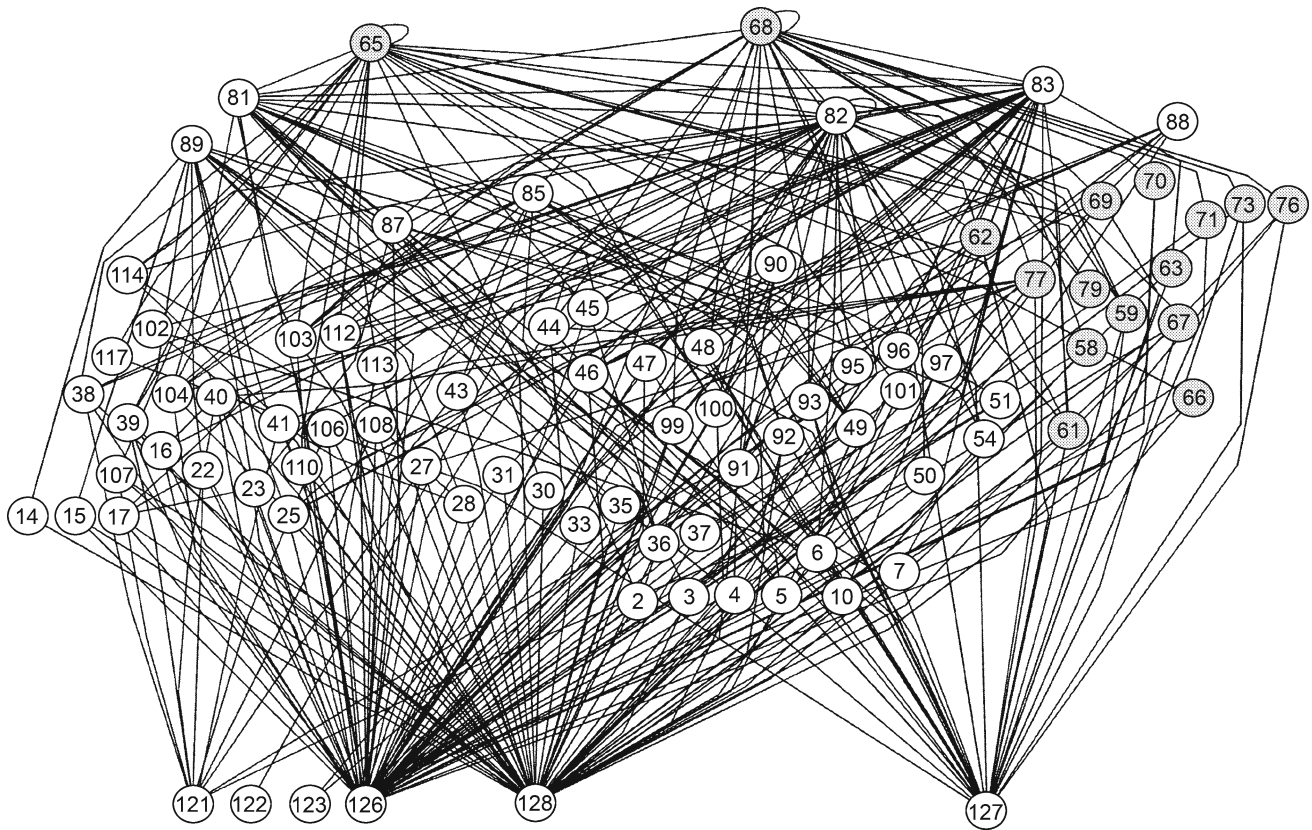


Fig. 12.1 Connectivity food web for the invertebrate community in Broadstone Stream, England in the autumn of 1996. Numbers represent consumers and resources: Protozoa: 1–10. Turbellaria: 11. Rotifera: 12–37. Nematoda: 38–41. Oligochaeta: 42–48. Tardigrada: 49–50. Acari: 51–56. INSECTA: Odonata: 57 *Cordulegaster boltonii*; Plecoptera: 58 *Leuctra nigra*, 59 *Leuctra hippopus*, 60 *Leuctra fusca*, 61 *Nemurella pictetii*, 62 *Siphonoperla torrentium*, 63 Plecoptera larvae, 64 *Leuctra nigra* adult; Trichoptera: 65 *Plectrocnemia conspersa*, 66 *Potamophylax cingulatus*, 67 *Adicella reducta*; Megaloptera: 68 *Sialis fuliginosa*; Coleoptera: 69 *Platambus maculatus*, 70 Helodidae sp., 71 Elmidae sp.; Diptera: Ceratopogonidae 72 *Bezzia* sp.; Tipulidae: 73 *Limonia* sp., 74 *Limonia modesta*, 75 *Dicranota* sp., 76 *Pedicia* sp., 77 *Limnophila* sp., 78 *Hexatoma* sp., 79 Limoniinae Gen. sp.; 80 *Rhypholophus* sp.; Chironomidae: 81 *Macropelopia nebulosa*, 82

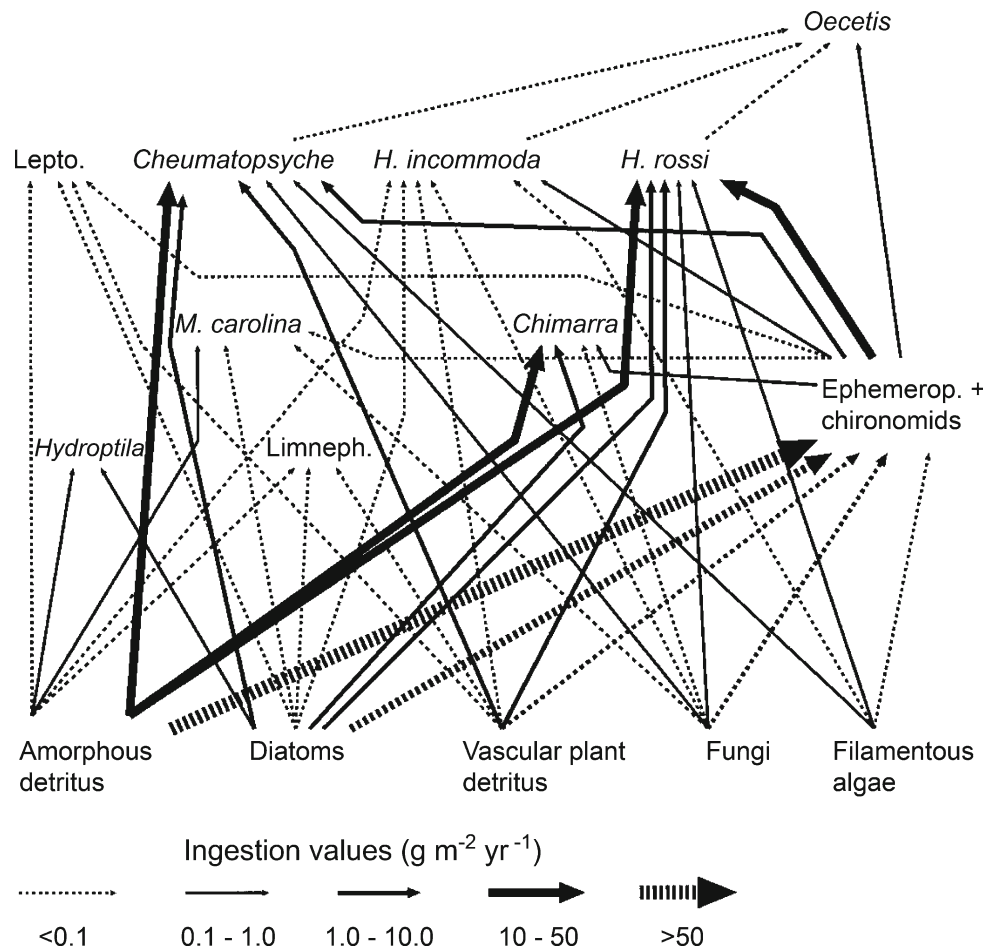
Trissopelopia longimana, 83 *Zavrelymyia barbatipes*, 84 *Conchapelopia viator*, 85 *Apsectrotanytus trifascipennis*, 86 *Zavrelymyia* sp. 2, 87 *Paramerina* sp., 88 *Krenopelopia* sp., 89 *Pentaneura* sp., 90 *Natarsia* sp., 91 *Prodiamesa olivace*, 92 *Brillia modesta*, 93 *Heterotrissocladius marcidus*, 94 *Heterotanytarsus* sp., 95 *Eukiefferiella* sp., 96 *Geothrocladius luteicornis*, 97 *Corynoneura lobata*, 98 Chironomus/Einfeldia sp., 99 *Polypedilum albicorne*, 100 *Micropsectra bidentata*, 101 *Mectricnemus* sp. Adult; Simuliidae: 102 *Simulium* sp. CRUSTACEA: Ostracoda:103; Cladocera:104–105; Copepoda: Cyclopoida: 106–111; Harpacticoida: 112–116; Algae and Plant material: 118–123. Various: 123 Plecoptera eggs, 124 Turbellaria eggs, 125 Rotifera eggs, 126 Fine particulate organic matter (FPOM), 127 Coarse particulate organic matter (CPOM), 128 *Leptothrix ochracea*. (Reproduced from Schmid-Araya et al. 2002)

Measurement of energy flux provides a quantitative assessment of the strength of linkages along each pathway. Figure 12.2 shows a less detailed food web, but one that quantifies organic matter pathways by converting information from gut analyses into annual ingestion rates for caddisfly larvae dwelling on snag habitat in the Ogeechee River in the southeastern US (Benke and Wallace 1997). The pathways from amorphous detritus and diatoms to several filter-feeding caddis larvae were particularly strong, but *Hydropsyche rossi* derived substantially more energy from consuming animal prey than did the other filter feeders.

12.1.1 Assessing Energy Flow Through Food Webs

As a food web essentially describes who eats what or whom, the construction of food webs requires information on diet. Traditionally, this has been inferred from general knowledge of trophic ecology (Chap. 9) or from detailed studies that combine gut analyses with estimates of assimilation efficiencies. More recently, feeding pathways have been inferred from chemical signatures in consumer tissues. These approaches are reviewed briefly below.

Fig. 12.2 Energy flow food web for caddisfly larvae in the Ogeechee River, Georgia, US. The width of the arrow reflects the magnitude of resources ingested. Abbreviations: Ephemeropt. = Ephemeroptera, Lepto. = Leptoceridae, Limneph. = Limnephilidae, *M. carolina* = *Macrostemum carolina*. (Reproduced from Benke and Wallace 1997)



12.1.1.1 Stable Isotopes and Other Dietary Indicators

Gut content analysis remains a widely used approach to the estimation of energy fluxes, despite the difficulty of identifying bits of soft-bodied prey and amorphous detritus, and the fact that it is extremely time intensive. To address some of these challenges, stable isotope analysis has become one of the primary methods to assess food resources, trophic position, and energy flow (Layman et al. 2012, 2015; Vander Zanden et al. 2016). Stable isotopes of carbon ($\delta^{13}\text{C}$), sulfur ($\delta^{34}\text{S}$), nitrogen ($\delta^{15}\text{N}$), hydrogen ($\delta^2\text{H}$) and oxygen ($\delta^{18}\text{O}$) can provide relevant information on major food sources, trophic level, and species movements. They are especially useful because they provide information about the type and location of resources that consumers use through time, generating spatial and temporal insights into trophic relationships and supporting the development of models of trophic structure (Layman et al. 2012).

The isotopes of different elements are analyzed to answer different questions. Carbon and sulfur isotopes are useful to determine food sources, because their isotopic ratios vary among primary producers. Nitrogen isotopes are useful to examine trophic relationships among species within a

community, because they change with each trophic transfer. Stable hydrogen isotopes can help to determine the relative contribution of allochthonous and autochthonous nutrient sources, and provide additional insights about trophic relationships. In combination with $\delta^2\text{H}$, $\delta^{18}\text{O}$ has the potential to generate information about food webs; however, oxygen isotopes are primarily affected by the source of water in a system rather than by diet (Vander Zanden et al. 2016). Stable isotope analysis can provide quantitative information about diet variation within a species, trophic composition, food chain length, and anthropogenically-derived shifts in community structure (Layman et al. 2012). In addition, other methods such as DNA sequencing of stomach contents or feces, fatty acids profiles, biomarkers, and stable isotopes of specific compounds can also be applied to quantify the composition of diet (Nielsen et al. 2018).

12.1.1.2 Secondary Production and Ingestion

Biological production is a measure of biomass produced within some component of an ecosystem. The most basic distinctions are between primary production, microbial production, and the production of all higher trophic levels, termed secondary production. Secondary production is the amount of

biomass produced by a population of a consumer species or consumer assemblage over some time period (Benke 1993). It is a net amount, with accrual due to growth and recruitment, and losses to mortality, including predation and disease, as well as emigration, emergence, and tissue loss during starvation or molting. It is a rate, often expressed on an annual basis. The growth of individuals depends on individual energy budgets and all of the environmental factors that affect an organism's metabolic balance. The growth of populations through reproduction and survival of recruits likewise depends on the many factors that influence the dynamics of populations. Thus, secondary production is an integrative measure that describes the amount of energy flowing through a population or assemblage at some location. When such information is available for the most common species in an assemblage, comparison of secondary production estimates provides a quantitative perspective on energy flow through that food web and its overall productivity relative to other studies.

The concept of secondary production can be further understood by noting the difference between biomass (B) and production (P). Biomass is the amount of living tissue present in the population at an instant in time (e.g., grams m^{-2}). Production is the amount of biomass produced over time (e.g., grams $m^{-2} yr^{-1}$). Their ratio, expressed as P/B, is referred to as biomass turnover or turnover rate, and has the units $time^{-1}$. Turnover rate is a measure of how rapidly growth and reproduction of a population generates new biomass. Fast growing and fast reproducing species, usually of small body size, may exhibit biomass turnover several to ten or more times in a year. Slow growing, slow reproducing species, usually of large body size, may turnover the population's biomass fewer than once per year (Benke and Huryn 2010).

Secondary production of a population is estimated by measuring population size, typically per unit of area or habitat, at frequent intervals, often monthly for aquatic insects, and converting numbers to biomass using published length–weight regressions (Benke 1993). Changes in monthly biomass are summed to provide an estimate of annual production. Alternatively, estimates of individual growth rates can be combined with biomass data. In an additional analysis, the relative contribution of each food web pathway to the secondary production of each species or taxon (analyses can be at the genus or family level) can be determined by quantification of gut contents and applying an estimate of assimilation efficiency to each food type. By quantifying both the secondary production and the contribution of each resource category to the energy assimilated by each of the most important members of an assemblage, one gains considerable insight into the relative importance of various pathways in food webs (Benke 2018).

12.1.2 Variability in Food Web Structure

Though freshwater food webs vary across space and time, they commonly are characterized by high generalism (each species has many food links) and redundancy (multiple species have similar trophic roles). They also typically contain a small number of larger predators in top trophic positions, and many smaller organisms as primary consumers. Cannibalism and mutual predation are also frequently documented in food webs (Ings et al. 2009). Yet, even though they often share many commonalities, food webs can be very diverse, particularly in their quantitative properties (e.g., abundance and biomass of resources and consumers, strength of interactions among species and resources) rather than in their composition, which can persist over time (Olesen et al. 2010).

Variability in food web structure arises from many environmental factors. In some cases, studies conducted over decades have detected changes in food webs due to variation in temperature, water chemistry, and the addition of top predators to a system (Woodward et al. 2010b; Layer et al. 2011). In an 18-year study of streams in California, US, Power et al. (2008) documented greater biomass of the filamentous green algae *Cladophora* in the spring of years when bankfull flooding occurred during winter months. They attributed greater algal biomass to reduced populations of predator-resistant grazers, such as the caddisfly *Dicosmoecus*, which was negatively impacted by high flows. In contrast, smaller winter floods or spring spates resulted in the short-distance downstream transport of *Dicosmoecus*, rather than increased mortality rates. Therefore, higher grazer abundance reduced biomass of *Cladophora* during the summer in lower-flow years. Food web interactions of fishes were also affected by flooding in this system. During post-flood periods, fishes had a stronger impact on benthic invertebrate populations than during drought years. Thus, flow-mediated changes in fish behavior also indirectly influenced algal populations.

In other cases, researchers have used space-for-time substitutions along a gradient of sites representing potential future conditions (e.g., water temperature gradients, urbanization gradients) to evaluate the responses of food webs to changing environmental conditions. For example, Woodward et al. (2010a) used geothermal streams with a water temperature gradient from 5 to 43 °C to assess the potential impact of climate change on trophic interactions in streams. Brown trout *Salmo trutta* fed on chironomids in the colder streams but fed primarily on the snail *Radix peregra* and the larval black fly *Simulium vitatum* in warmer streams. Trout were larger in warmer streams, suggesting that trout may shift their diet to larger prey in warmer systems to meet

higher metabolic demand. Similarly, researcher compared food webs of 20 streams along a pH gradient (5.0 to 8.4) to examine how changes in acidity influenced stream community interactions (Layer et al. 2013). Herbivore-detritivore generalists were found in each stream; however, these taxa were dominant in the more acidic sites. In less acidic (higher pH) streams, the diversity and biomass of algae and the abundance of specialist grazers increased. At higher pH levels, specialist grazers and herbivore-detritivores consumed more algae, indicating shifts in dominant basal food resources along an acidity gradient. This indicates that generalist species were able to shift from a detritus-dominant to an algal-dominant diet along a gradient of pH, and suggests the lack of specialist grazers in acidic streams may contribute to the slow recovery of streams to anthropogenically-derived acid deposition.

As discussed in detail in previous chapters, basal resources, productivity, and habitat conditions are all associated with position along a river continuum; hence, food web structure should also change with landscape position (Woodward and Hildrew 2002). Landscape features govern the physical characteristics of streams, influencing flow regime and habitat features, the relative importance of basal resources in food webs, the magnitude of external subsidies of nutrients, detritus, and prey, and conveying a high degree of individuality to the species assemblage and food web structure among locales (Woodward and Hildrew 2002). Models of stream ecology, particularly the river continuum concept (Fig. 1.1), attempt to explain variation in structure and function of stream communities due to longitudinal patterns and shifts in energy inputs between forested and open sites (Vannote et al. 1980). In brief, the river continuum concept predicts that allochthonous sources support food webs in low-order streams because of their small size and connectivity to terrestrial environments, autochthonous sources increase in importance in middle reaches as the river widens and shading of the river channel declines, and large rivers are strongly dependent on material exported from upstream and lateral connectivity. The influence of the riparian corridor on basal resource availability is well known, especially in small, temperate streams where the extent of summer shade, autumn leaf-fall, and spring leaf-out influence the patterns in allochthony and autochthony. In a study conducted in two Canadian rivers using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes, Hayden et al. (2016) observed that most invertebrate and fish consumers relied on autochthonous sources along the river network, except for shredder species, which primarily depended upon allochthonous organic matter.

Anthropogenic activities may also shift food web relationships with regard to allochthony and autochthony in river networks. Along the Pecos River, in the southwestern United States, East et al. (2017) found that in middle reaches of the river, fish and macroinvertebrate populations

consumed carbon from both autochthonous and riparian sources, and the food webs had few piscivorous species. However, in downstream reaches affected by salinization that was associated with flow alteration, food chains were shorter and consumers were predominantly supported by instream carbon sources. Reduced discharge and habitat availability likely were responsible, because flows became intermittent and reaches were reduced to isolated pools. Downstream, where the river receives perennial fresh inputs from springs, the authors documented decreases in salinity, increases in pool habitats, and a return to longer food chains and dependence on both allochthonous and autochthonous resources, reflecting a discontinuum along the Pecos River.

Urbanization may also affect stream trophic structure (El-Sabaawi 2018). Primary production in urban watersheds can be impacted by increased nutrient loading and by the reduction of shade as riparian forests are removed for development. Increases in the intensity of storm discharge can scour streambeds, removing algae and displacing grazing invertebrate species. Changes in riparian plant composition through the introduction of species, wastewater introduction through aging and obsolete infrastructure, and the loss of sensitive herbivorous and detritivorous species can also change basal food resource availability and consumer diversity and abundance in urban streams. For example, using stable isotope analysis to examine differences in aquatic communities receiving wastewater discharge, Singer and Battin (2007) found that sewage-derived particulate organic matter doubled macroinvertebrate secondary production relative to reaches without discharge.

12.1.3 Factors Influencing Secondary Production

Organisms of small body size typically exhibit rapid growth and development, have short life spans, and have multiple generations per year relative to those of large body size. This is illustrated in Fig. 12.3 for several aquatic insect taxa in a tropical stream where warm temperatures and small body size result in very high growth rates (Hall et al. 2011). It is also well established that ectotherms generally exhibit more rapid growth with increasing temperature. The relationship between body size, body temperature, and metabolic rates, and the tendency for small-bodied organisms to have higher mass-specific metabolic rates than larger-bodied organisms, leads to predictions about the scaling of secondary production measures to body size. Estimates of total invertebrate secondary production ranged from 5 to 25 $\text{g m}^{-2} \text{yr}^{-1}$ based on a review of a number of studies of low-order streams in North America (Walther and Whiles 2011), although higher values have been recorded (Benke 1993). The turnover rate (P/B) of biomass for a single generation (cohort) of an

individual species often is roughly five (Benke 1993), and so a population with an annual life cycle will have an annual P/B of roughly five as well. A population with two cohorts per year will have an annual P/B of about 10, and small-bodied, very fast growing species may have an annual P/B of 20 or more. Indeed, estimates of annual biomass turnover rates for individual species of benthic freshwater macroinvertebrates vary widely, with the majority between two and 20, but both lower and higher values have been reported. The entire macroinvertebrate assemblage at a site will include both slow and fast-growing species, and so assemblage P/B will tend towards intermediate values.

The influence of temperature on the variation in secondary production among populations is clearly evident from estimates of fish assemblage production across cold, cool, and warm water streams of the Appalachian Mountains, US (Myers et al. 2018). Only two streams in this study were considered warm-water, and they had higher biomass and production. Production-to-biomass (P/B) ratios ranged from 0.20 to 1.07, similar to other reported studies, although some higher values have been reported elsewhere. As the mean P/B for all 25 streams combined was 0.65, these fish assemblages turned over more than half of their total biomass annually. A synthesis of a large data base of fish production studies estimated a median P/B for fish assemblages at 0.86 and for individual species of 1.2, indicating that most freshwater fish communities and populations of

single species turn over approximately annually (Rypel and David 2017). Their synthesis of a large number of studies indicated that fish assemblage production showed a decreasing trend with higher latitude. However, much scatter was evident across intermediate (temperate) latitudes, possibly due to local differences in ecosystem productivity and fish assemblage diversity. Individual species may exhibit a counter-gradient trend of production with latitude, suggestive of physiological adaptation for faster individual growth rates during short growing seasons.

In addition to temperature and body size, which exert fundamental control over secondary production and turnover rates, species are likely to be influenced by a wide variety of environmental factors. Reflecting the truism that species are most successful in those environments to which they are best adapted, and do less well in environments that we call marginal based on species' performance, much variation in secondary production estimates no doubt reflects the environmental conditions under which production is measured. By the same token, secondary production serves as a useful measure of suitable conditions, identifying productive habitats for a species. In essence, all of the environmental variables that influence individual growth and reproduction, and the dynamics of populations, will also influence secondary production (Patrick et al. 2019).

Numerous studies have documented variation in secondary production of aquatic invertebrates in response to habitat conditions. Sampling of different habitats allows a weighted-area estimate of total invertebrate production and provides insight into the relative importance of different habitat types for different functional groups. Comparing bedrock-outcrop, riffle, and pool habitats in an Appalachian mountain stream in the southeastern US, Huryn and Wallace (1987) found highest production of collector-filterers in bedrock-outcrop habitats, followed by riffles, and then pools, whereas shredders showed the opposite, and scrapers were most productive in riffle habitats. Annual invertebrate production on a floodplain continuously inundated over nine months was several-fold higher than one flooded only occasionally during storms, and floodplain production was one to two orders of magnitude higher than in channels (Gladden and Smock 1990). Annual production of macroinvertebrate communities along a first- to seventh-order river continuum in the southern Appalachian Mountains, US, displayed large variation among habitats (Fig. 12.4; Grubaugh et al. 1997). Production was relatively low in depositional habitats and some gravel substrates, greater in bedrock habitats, and greatest on plant-covered cobbles, which can stabilize the substrate and enhance access of collector-filtering invertebrates to entrained food resources. After accounting for the proportional availability of habitats along the continuum, estimates of total production increased significantly with stream size. Annual production estimates for sixth- and seventh-order reaches

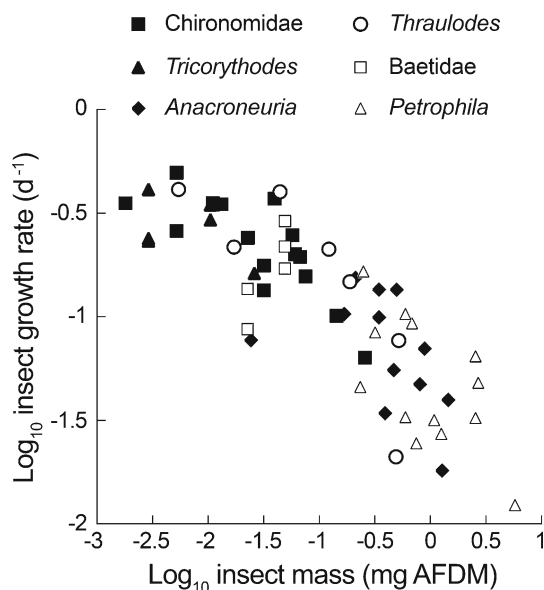
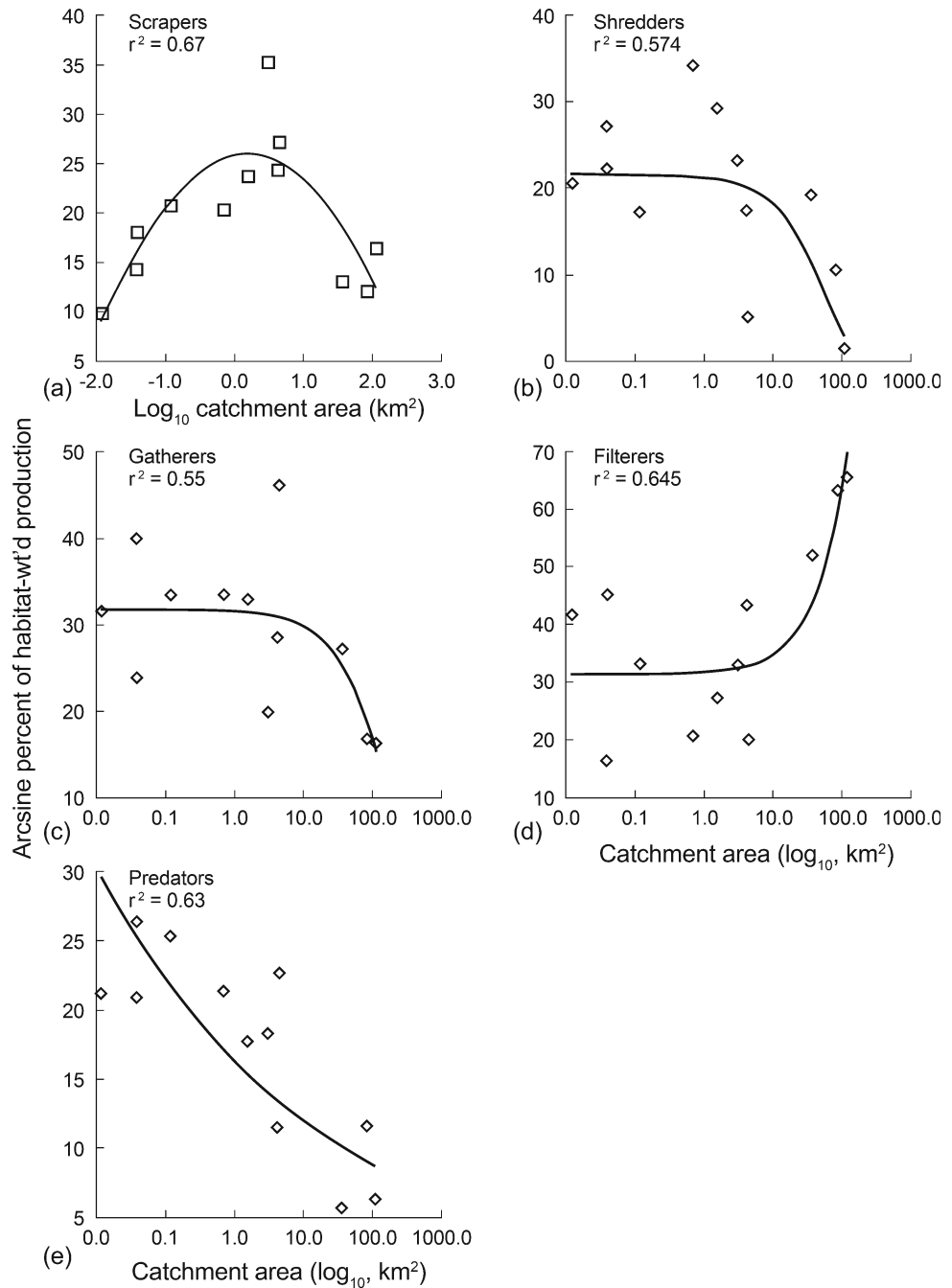


Fig. 12.3 Insect specific growth rates declined with body size in in-stream incubations. Growth rates were estimated using 1–5 individuals that were incubated in a mesh container between 3–7 days. For smaller individuals, 3–4 individuals were incubated together. Each point represents a mean value collected from 3–6 individuals in cages, or from individual organisms (i.e., *Anacroneria* and *Petrophila*). (Reproduced from Hall et al. 2011)

Fig. 12.4 Estimates of the relative contributions of functional feeding groups to habitat weighted, secondary production in the benthic macroinvertebrate community along the Ball Creek-Coweeta Creek-Little Tennessee River continuum in the southeastern US. The contributions of the feeding groups are depicted as percentages of total habitat-weighted production at each site. The data were arcsine transformed before plotting. The lines represent the best-fit relationships between the catchment area and the contribution of each functional feeding group to production: (a) scrapers, (b) shredders, (c) gatherers, (d) filterers, (e) predators. (Reproduced from Grubaugh et al. 1997)



were amongst the highest reported for lotic systems. Moreover, production estimates for individual functional feeding-groups, estimated by proportional habitat weighting, generally supported predictions of the river continuum concept.

12.1.4 Spatial Subsidies and Aquatic Community Response

Evidence from a variety of ecosystems reveals that nutrients and energy flowing across habitat boundaries, or spatial

subsidies, can fundamentally alter food webs and biogeochemical cycling in recipient ecosystems (Fig. 12.5; Polis et al. 1997; Polis and Hurd 1996). In its inception, spatial subsidies were defined as a donor-controlled resource (e.g., animal tissue, leaf litter and other plant tissues, etc.) moving from one habitat to another, resulting in greater system productivity and affecting consumer–resource dynamics (Layman et al. 2015). Energy flow across habitat boundaries has been a central point of discussion in stream ecology for many decades. Likens and Bormann (1974) were amongst the first to quantify the influence of terrestrial inputs of

nutrient and organic matter on ecosystem function in streams. Foundational concepts in stream ecology, including the river continuum (Vannote et al. 1980) and flood-pulse (Junk et al. 1989), focus on in-stream energy supplies that depend upon the flow of materials between terrestrial and aquatic environments. Food web studies have added significantly to our understanding of the magnitude of various subsidy pathways and how these pathways differ in importance with environmental context, particularly landscape setting. Energy subsidies to fluvial ecosystems that can be extremely important to ecosystem metabolism include leaf litter, the infall of terrestrial invertebrates, and the carcasses and reproductive products of migrating fishes.

Spatial subsidies are expected to have their greatest influence on aquatic communities and ecosystem processes when the donor and recipient systems substantially differ in their productivity, such that resources move from a highly productive system to a system of much lower productivity (Layman et al. 2015). Additionally, the characteristics of the boundary between donor and recipient systems will influence the lability, quantity, timing, and duration of a subsidy entering the new system (Subalusky and Post 2019). In streams, the perimeter: volume ratio may be especially relevant in understanding the potential influence of terrestrially-derived subsidies on rivers and streams. As highlighted in the river continuum concept, energy dynamics in smaller, headwater streams in forested regions of the world are expected to be fueled by allochthonous inputs from riparian vegetation, whereas floodplain subsidies can be important to lowland rivers with intact floodplains.

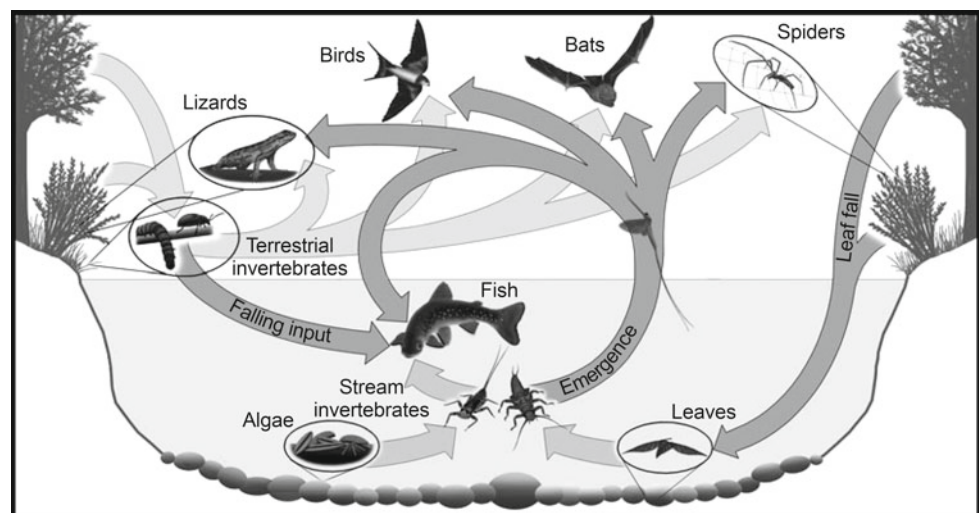
Allochthonous inputs of leaf litter and other plant products, extensively reviewed in Chap. 7, are an important and well-studied terrestrial subsidy to aquatic ecosystems. However, except in the case of migrating fishes, animal-derived subsidies have received less attention. In a recent review of

the effects of animal-derived subsidies, Subalusky and Post (2019) developed a conceptual model (Fig. 7.1) describing the ways in which the net impact of subsidies on stream ecology is influenced by the characteristics of the resources crossing ecosystem boundaries, and the size, species diversity, productivity, resource availability, and seasonality of both the donor and recipient systems. In this model, lability (referring to resource quality), quantity, timing, and duration of material moving from a donor to a recipient system, and the characteristics of both the donor and recipient ecosystems, determine if the material crossing ecosystem boundaries functions as a subsidy, and whether it enhances or reduces productivity. Subsidy flow between systems can occur passively, through wind, atmospheric deposition, overland flow, and downstream flow; or by active processes including animal movement and from anthropogenic sources such as wastewater discharge (Subalusky and Post 2019).

Downstream transport of nutrients and organic matter by river flow and lateral exchanges with the floodplain during seasonal inundation are dominant physical processes by which subsidies are delivered. Increasing evidence suggests that animal-mediated subsidies are diverse and support essential biogeochemical processes in lotic environments (Flecker et al. 2010). Subsidies introduced through animal movement are often rich in limiting nutrients, such as nitrogen and phosphorus. Additionally, many species have the ability to move upstream, bringing resources from downstream locations.

Anadromous and catadromous species that move between freshwater and marine environments, such as salmon, transfer marine-derived nutrients into freshwater systems (Levi et al. 2013; Tiegs et al. 2011; Holtgrieve and Schindler 2011). Salmon carcasses even provide a subsidy to riparian areas, seen in the growth of streamside trees, as a result of carcasses moved onto stream banks by predators and floods

Fig. 12.5 Generalized conceptual model of reciprocal flows of spatial subsidies (i.e., invertebrate prey and inputs of plant material) that have direct and indirect effects in both stream and riparian food webs. (Reproduced from Baxter et al. 2005)



(Hocking and Reynolds 2012). Additionally, animals that move between terrestrial and aquatic environments via shifts in ontogeny, such as amphibians and many aquatic insects, or through daily migrations, such as hippos, actively move energy and nutrients across habitat boundaries [e.g., amphibians (Capps et al. 2015b; Luhring et al. 2017), hippos (Dutton et al. 2018)]. Large herds of migrating animals can also introduce vast quantities of energy and nutrients to river systems via mass drowning events (Wenger et al. 2019; Subalusky et al. 2017).

Inputs of terrestrial insects can be an important energy subsidy to top consumers such as fishes, as Nakano et al. (1999) demonstrated by placing a fine-mesh net over a forest stream in Japan. The exclusion of terrestrial invertebrates resulted in greater fish predation on benthic aquatic invertebrates, triggering a trophic cascade and an increase in periphyton biomass. Further, the biomass of herbivorous invertebrates and periphyton did not differ between treatments with or without fish when terrestrial invertebrate inputs were allowed, suggesting that the supply of arthropods from land normally prevented strong top-down control (Baxter et al. 2005). The complicated consequences for food web interactions due to external subsidies is also evident in a competitive shift in feeding by native Dolly Varden charr *Salvelinus malma* in northern Japan in response to non-native rainbow trout (Baxter et al. 2004). Trout were better able to consume the terrestrial invertebrates that fell into the stream, forcing charr to feed on herbivorous invertebrates and resulting in an increase in periphyton biomass. However, the biomass of adult aquatic insects emerging from the stream decreased, and this in turn reduced the density of spiders in the riparian forest.

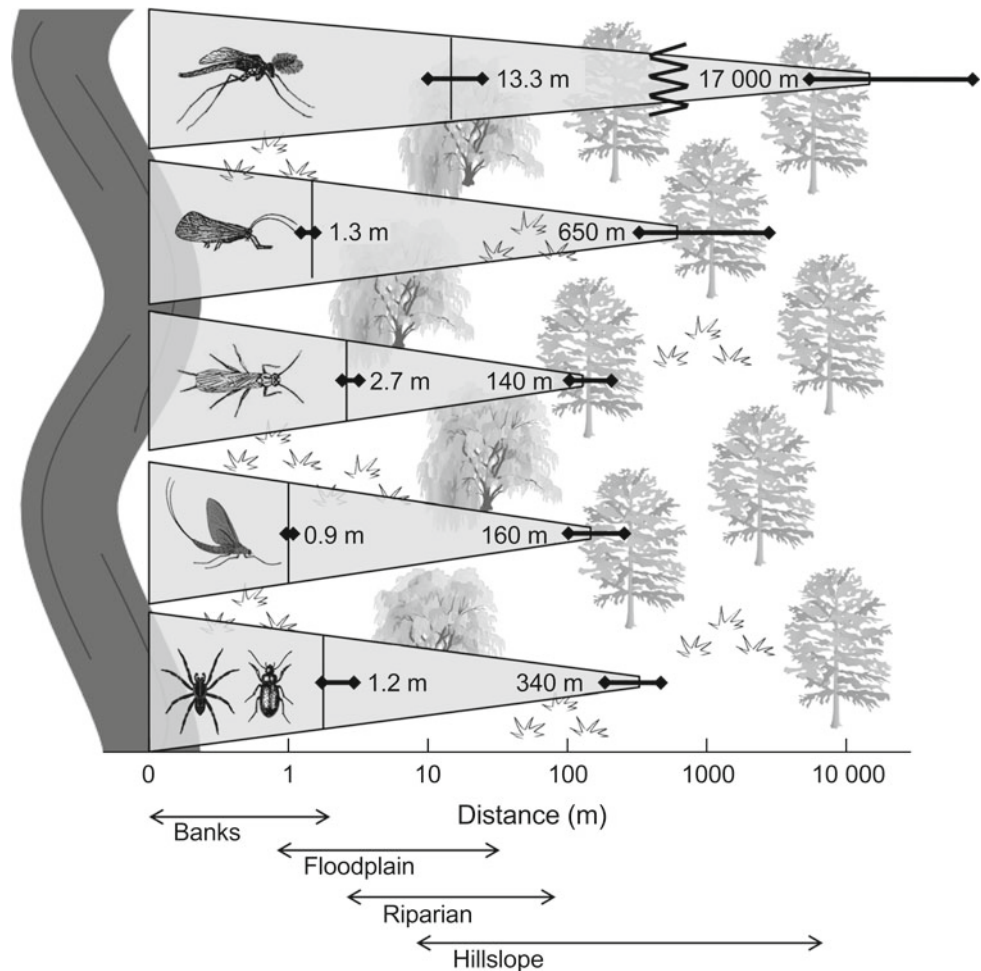
Subsidies can also travel from streams to the surrounding riparian area, as exemplified by the dependence of spiders and lizards in riparian zones on the emergence of aquatic insects, which can provide 25–100% of the energy required by those animals (Sabo and Power 2002; Baxter et al. 2005). Even the frequency of pollinator visits to riparian plants can be affected by fish predation on larval odonates, which determines the abundance of adult dragonflies and hence predation pressure on pollinating insects (Knight et al. 2005). Some riparian predators, like the fishing spider, lurk at the water's edge (Fig. 12.6), but aquatic subsidies can extend some distance into the riparian zone. Muehlbauer et al. (2014) defined the “stream signature” as the distance from the stream at which terrestrial organisms are receiving aquatic subsidies. The 50% signature refers to the distance where half of the food web energy of organisms within the terrestrial ecosystem comes from stream subsidies. In their analyses, the 50% signature was at 1.5 m, suggesting that most aquatic insects stay near the streams and most recipients are also near the stream. However, the 10% signature was at 550 m, indicating that a fraction of stream subsidies extends much farther. Notably, the signatures vary among aquatic and terrestrial taxa, and chironomids, or midges, had the largest stream signature (Fig. 12.7).

For migratory and mobile species, stable isotope analysis has been useful in determining the location where carbon was assimilated, thus providing insight into the magnitude of cross-system subsidies. Differences in the $\delta^{13}\text{C}$ of muscle tissue in the migratory tropical fish *Semaprochilodus insignis* established that carbon produced in blackwater systems contributed to fish stocks harvested from whitewater systems of the Amazon (Benedito-Cecilio and Araujo-Lima

Fig. 12.6 A fishing spider (*Dolomedes*) hunts near the water's surface in a Costa Rican stream, as a group of Creek Tetras (*Bryconamericus*) swim below the surface. Photo by David Herasimtshchuk, Freshwaters Illustrated



Fig. 12.7 Estimates of the distance subsidies travel into recipient landscapes, or “stream signatures” for different organisms. The values listed for each group of organisms represent the distances at which the abundance of a given group are the 50% and 10% of its near-stream levels. The horizontal lines depict the confidence intervals for each distance. Moving from the bottom to the top of the figure, the organisms are: terrestrial predators (webbed spiders, ground/hunting spiders and predaceous beetles [Coleoptera]), mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), and midges (Chironomidae). The jagged line documents the furthest distance midges were collected in the study; therefore, distances past this point should be evaluated with caution. (Reproduced from Muehlbauer et al. 2014)



2002). Because epilithic algae, detritus, and algal filaments varied in abundance among benthic habitats and streams in the headwaters of the Eel River of northern California, Finlay et al. (2002) were able to use carbon isotope ratios to assess habitat use by different consumers. The $\delta^{13}\text{C}$ values of collector-gatherers and scrapers indicated a reliance on algae from local sources within their riffle or shallow pool habitats, whereas filter feeders derived more carbon from upstream shallow pools. Algal production from shallow pools was the dominant resource base for vertebrate predators in late summer regardless of the habitat where they were collected. The drift of pool insects into riffles, rather than movement of trout among habitats, was the presumed mechanism, illuminating between-habitat subsidies similar to cross-ecosystem subsidies.

12.1.5 Flow Food Webs and Ecosystem Processes

A flow food web constructed from annual production of consumers, proportions of food categories consumed, and

assimilation efficiencies for the different food types not only provides insights into basal resources, as described above, but also allows a detailed description of energy flow between resources and consumers (Marcarelli et al. 2011; Benke 2018). Figure 12.8 illustrates how the magnitude of flows between basal resources and consumers, indicated by thickness of arrows, reveals which consumer taxa have assimilated the greater fraction of energy available from each basal resource. As Hall et al. (2000) point out, their food webs encompassed most (84–91%) of invertebrate secondary production, but less than 30% of the estimated total links, which would require data for a large number of rare taxa. Because they assessed diets of invertebrates responsible for some 80–90% of total production, it seems likely that omission of rare taxa is not a hindrance in food web analysis.

Flow food webs for multiple sites along the Little Tennessee River, North Carolina, US, were structurally similar, because the sites had similar taxa and resources (Rosi-Marshall and Wallace 2002). However, the rates of secondary production of the taxa and the form of the dominant resource differed, and so these structurally similar webs were functionally very different. What was consumed, the

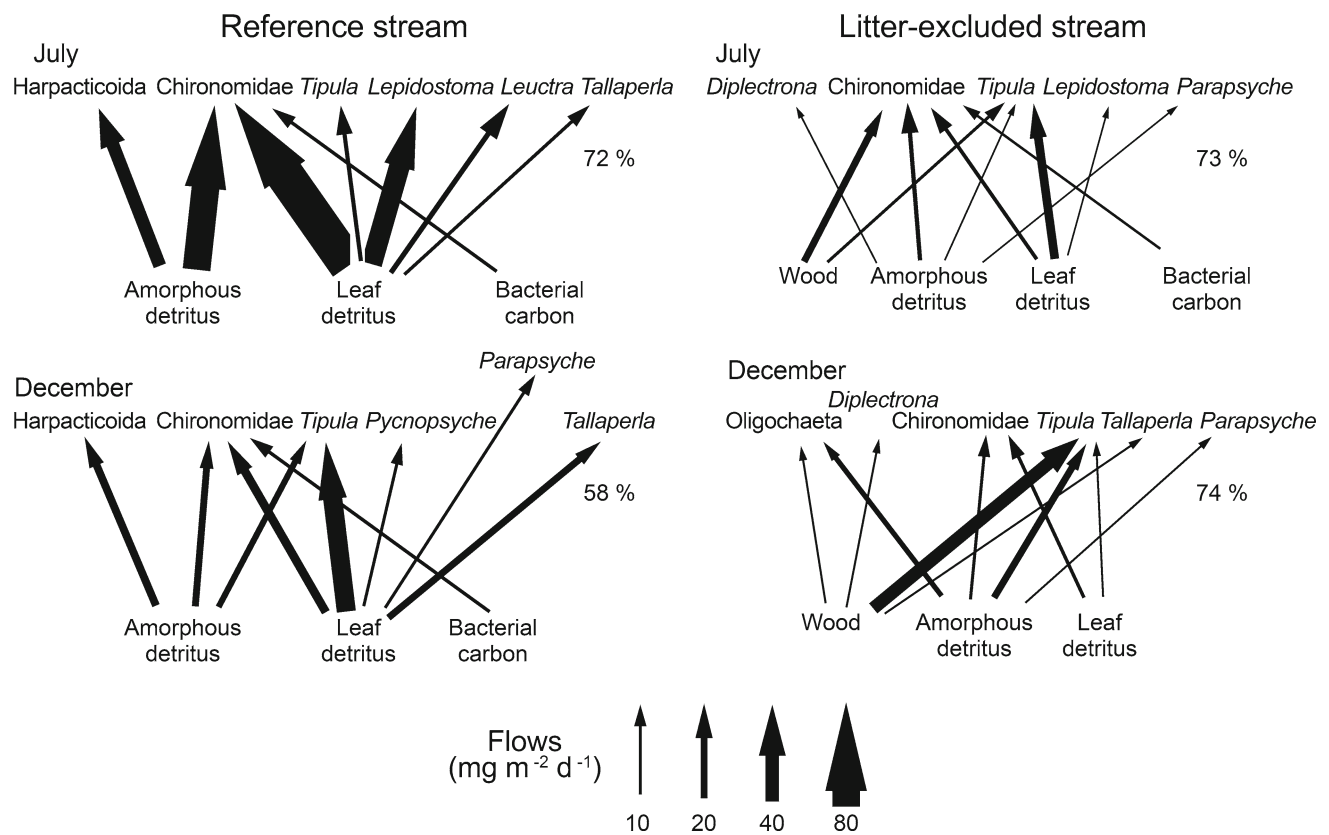


Fig. 12.8 Comparison of energy flows through stream food webs in reference streams and streams where leaf litter was experimentally excluded. The top panels represent the months of December. The percentage values on the right side of each food web are the

percentages of organic matter flow represented in the diagram. The width of the arrows is proportional to the magnitude of the flows. (Reproduced from Hall et al. 2000)

rates at which food resources were consumed, and which taxa dominated the consumption of resources all differed along the river gradient.

The magnitude of individual energy flow pathways within a food web can be quantified from estimates of secondary production and food ingestion, as described earlier. Such quantification of energy flow among species and between trophic levels in an assemblage is significantly more informative than food web diagrams that simply show who eats whom, known as connectivity or linkage webs (Fig. 12.1). Although labor intensive, once such data are obtained, they can be used to answer at least three questions (Benke 2018). By comparing the amount of secondary production that is fueled by different basal resources, secondary production reveals the trophic basis for production. By comparing the magnitude of linkages from basal resources through primary consumers to predators, an energy flow food web reveals the dominant energy pathways and dominant actors in the web. Trophic position can be estimated by averaging all flow pathways, which is especially advantageous with omnivores. Finally, by comparing the amount of biomass consumed by a predator to the

production of its prey, one derives a measure of interaction strength, and possible top-down control. In this regard, food web analysis is an alternative to experimental manipulation as a way to detect strong interactors in a food web, and has an advantage in that experimental manipulation of all possible linkages is impractical or infeasible.

Flow food webs can be very detailed. The highly resolved snag web reported by Benke (2018) contained 462 quantified links $\geq 1 \text{ mg m}^{-2} \text{ yr}^{-1}$. Detailed flow food webs were also constructed for invertebrate assemblages in experimental stream channels in southern England, which were subjected to simulated intermittent drought by 6-days of dewatering per month (Ledger et al. 2013a; Ledger et al. 2013b). Biomass fluxes from detritus were responsible for 96% of all energy transfers, including to predators, and just 5% of links accounted for 90% of biomass flux. As also seen in the Hall et al. (2000) study, the flow food web for just the dominant pathways provides an adequate description of the major linkages (Fig. 12.9). Experimental exposure to drought reduced the biomass flux by more than half, and resulted in substantial losses of species and links, especially among predators.

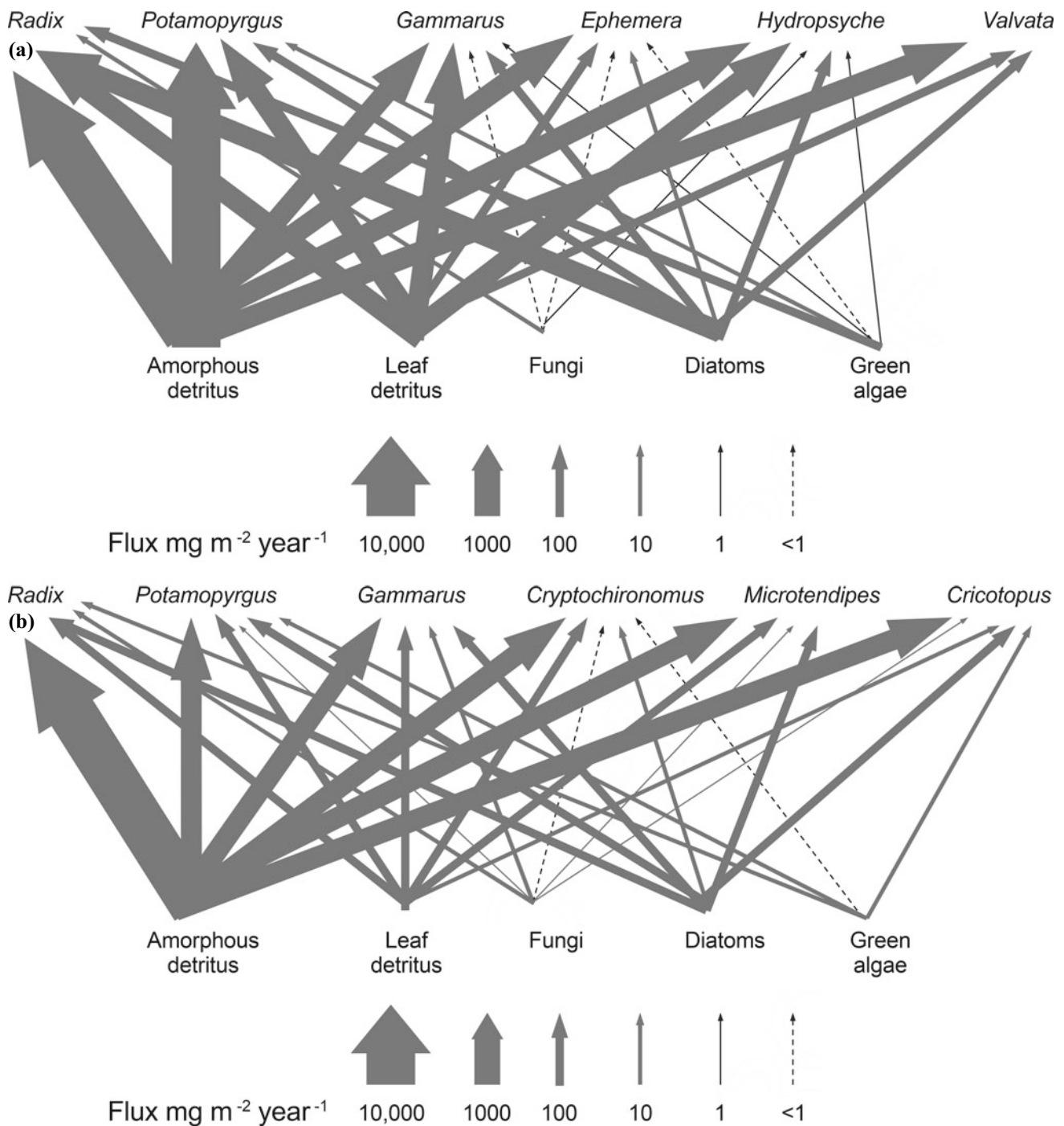


Fig. 12.9 Biomass fluxes from resources to consumers in a experimental manipulation to assess the effects of drought. The fluxes in (a) are from control treatments and in (b) are from drought-disturbed

treatments. The width of arrows are proportional to the size of the annual flux on a per area basis. (Reproduced from Ledger et al. 2013a)

The information in a flow food web also can be used to assign taxa to trophic levels. Owing to omnivory and the utilization of resources at different trophic levels, species often cannot be assigned to an integer trophic level. Rather than using a linear sequence of trophic links, in which the placement of omnivores is problematic, trophic position

(TP) can be determined from the trophic positions of all food resources consumed by a particular species, providing a mean estimate of how many links that species is removed from its basal resources. Trophic position above basal resources (assigned level 1) and their primary consumers (level 2) is calculated using the fractional amount of each

food type assimilated by each consumer and TPs of all such food items. Using this approach, trophic categories and positions estimated from ingestion and production are fewer than reported for integer-based food chains. The snag food web analyzed by Benke (2018) had seven integer trophic levels based on linkages, but estimated trophic positions ranged only between 1.0 to 3.69. Most link-three species had calculated trophic position only slightly greater than two, and link-five species were only slightly above trophic position three.

Strengths of interactions within a flow food web can be estimated in biomass terms by dividing the rate of organic matter flux of a given food resource to a consumer by the production rate of that resource (Marecchelli et al. 2011; Benke 2018). Ingestion divided by production (I/P , both in units $\text{mg m}^{-2} \text{yr}^{-1}$, hence dimensionless) is estimated by dividing a predator's consumption of a given prey by that prey's production, providing a direct measure of predator impact. It thus is a measure of top-down interaction strength, typically used to determine predator impact on their prey base. This serves as an alternative to experimental manipulations, which have long been the traditional approach for estimating per capita interaction strength. A study from rocky intertidal habitat found that interaction strength estimated from secondary production data compared well with experimental findings (Wootton 1997).

Estimates of interaction strength have been used to identify strong and weak interactions within food webs, to assess how interaction strength can change with environmental conditions, and to make inferences about the relative importance of top-down versus bottom-up control over food webs. In Benke's (2018) analysis of the snag web, most impact measures were weak, implying that most predators had little effect on their prey. Other studies have found weak I/P to be common and strong interactions to be less so (Woodward et al. 2005; Cross et al. 2013).

Predator control of prey was stronger when basal resources were reduced in a whole-stream litter exclusion experiment (Hall et al. 2000). Because fewer prey taxa were available in the litter-excluded stream, the dominant flows were from the remaining common prey taxa to predators. In the reference stream with more prey available, predation likely was more diffuse and thus interaction strengths less strong. Interaction strengths were markedly different in food webs of the Colorado River among locations stretching 386 km within the Grand Canyon, Arizona, US (Cross et al. 2013). A few energy pathways dominated at upstream sites (from diatoms to a few invertebrate taxa to rainbow trout), energy efficiencies were low as only about 20% of invertebrate production was consumed by fishes, and the web showed a small number of relatively high interaction strength links. Farther downriver, invertebrate production was much lower, detritus was a more important basal

resource, energy transfer to higher trophic levels were more efficient, and food webs exhibited a higher frequency of weak interactions, defined as consumption/production < 0.1 ($< 10\%$).

In any system where inputs and exports of organic matter and organisms are relatively modest, one expects the energy produced at lower trophic levels to be consumed by the ingestion and secondary production of higher trophic levels. In a leaf-litter exclusion study, predator production varied in accord with non-predator production (Wallace et al. 1997). Unsurprisingly, more energy produced at lower trophic levels generally results in more energy consumed at higher trophic levels. However, studies have reported that predators consume essentially all secondary production, only a small fraction of secondary production, or even that the food supply appears inadequate to support predator production. In a much cited example of the latter, based on study of the trout population of the Horokiwi stream in New Zealand, Allen (1951) noted an apparent paradox: the biomass of the trout population of this stream appeared to be much greater than its food supply could support. This came to be known as the Allen paradox and led to much further research into energy supply to top consumers.

There has to be an answer, of course, and eventually it came in three forms. First, evidence accumulated that aquatic food webs can receive external subsidies in the form of invertebrate prey entering streams from the surrounding riparian area (Baxter et al. 2005). Second, invertebrate production may previously have been underestimated, based on evidence that production and turnover (P/B ratios), especially of smaller invertebrates, can be higher than previously thought (Benke and Huryn 2010). Third, better accounting showed that, as one would expect, the productivity of lower trophic levels does provide a sufficient food supply for higher consumers, who may indeed consume all or nearly all of available secondary production. A comprehensive production budget for a trout stream in the southeastern part of South Island, New Zealand, similar in productivity to the Horokiwi stream, included estimates of primary production, production by brown trout and surficial and hyporheic macroinvertebrates, input of terrestrial invertebrates, and cannibalism by trout (Fig. 12.10; Huryn 1996). Food sources were indeed adequate to support a trout population typical of highly productive streams, but only when all budget compartments, including external inputs, were accounted for in the analysis.

When the highest trophic level consumes almost all of the secondary production of the trophic level below, and the lower trophic level consumes only a modest fraction of its basal resources, top-down control is strongly implicated. This appears likely in Huryn's (1996) study, as secondary production by aquatic invertebrates required only about 20% of total primary production, implying top-down control of

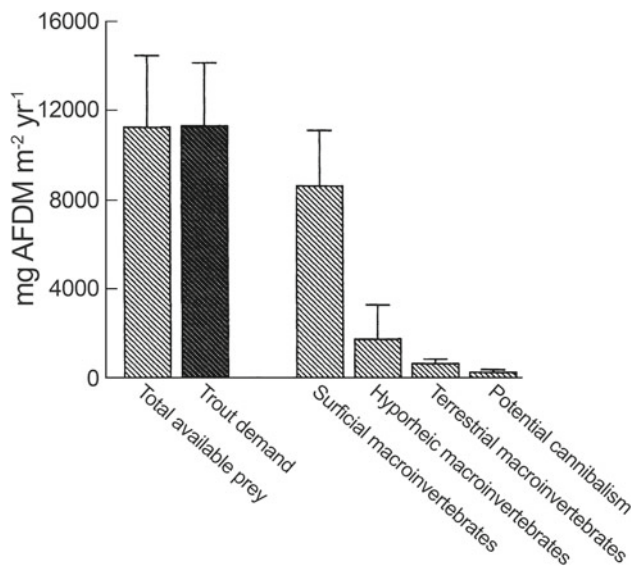


Fig. 12.10 Annual production estimates of the prey available for trout and source-specific prey availability. Trout demand was calculated using published data about the ecological efficiency of trout. The error bars depict 95% confidence intervals. (Reproduced from Huryn 1996)

invertebrates by trout. The inference of strong top-down control in productive New Zealand trout streams gained additional support from studies showing that macroinvertebrate biomass decreased markedly and periphyton biomass increased in experimental enclosures with trout (Flecker and Townsend 1994).

However, it is by no means assured that predators will have strong top-down influence. Production budgets for a New Zealand stream inhabited by native river galaxias (*Galaxias eldoni*) differed from trout stream budgets (Huryn 1998). Fish consumed approximately 18% of available prey production, and invertebrates consumed approximately 75% of primary production. Unlike the trout stream, which provided strong evidence of top-down control and surplus primary production, the galaxias stream likely experienced a mix of top-down and bottom-up controls, in which primary and secondary production were presumably mutually limiting. Experimental studies again were supportive, as the influence of galaxias in enclosures was less strong than the effect of trout (Flecker and Townsend 1994). In the snag food web reported by (Benke and Wallace 2015), invertebrate predators and omnivores consumed about 60% of all invertebrate production, implying that the remainder is available for fish consumption, adult emergence, and other mortality. Most fish predation presumably occurs when invertebrates depart from a snag into the drift, which could indicate that fishes are limited by their food supply rather than the reverse.

The ability of I/P estimates and related calculations to resolve the strength of predator control may be limited to some degree by measurement precision. Huryn's (1996) results suggesting that trout consumed 100% of prey

production raises a different question, namely what insect production remains available for the aerial stage's emergence and reproduction? Studies suggest that as much as 20% of production may be lost to emergence (Jackson and Fisher 1986; Statzner and Resh 1993) although it probably could be quite a bit less. Some mortality may be difficult to capture in budget calculations, including loss to parasitism and disease, burial in sediments, and so on. While comparative inferences among various pathways no doubt reveal which species are the strong interactors, and top-down control is highly likely when predators consume 80% or more of secondary production, measurement error cannot be discounted when making inferences from budget comparisons that have so many terms to estimate.

Anthropogenic activities have been shown to alter the flow of energy and nutrients through food webs. Reductions in secondary production of heptageniid mayflies provided evidence of the effects of chronic metal contamination on insect populations in Rocky Mountain (US) streams (Carlisle and Clements 2005, 2003). Using two measures of urban nonpoint pollution, stream-water conductivity and nutrient concentrations, Johnson et al. (2013) reported a decline in species richness but an increase in total invertebrate production, due to pollution-tolerant non-insect taxa (e.g. Oligochaeta, *Gammarus* sp., *Lirceus* sp., *Physa* sp.), some of which are resistant to macroinvertebrate predation.

12.2 Aquatic Communities and Ecosystem Function

Intact biological assemblages carry out various ecosystem processes including primary production, organic matter decomposition, nutrient cycling, and secondary production. This is thought to be the consequence of the presence of a diverse mix of species with different functional capabilities, and perhaps also with some level of functional redundancy that conveys resiliency in the face of an ever-changing environment. As species are lost from ecosystems due to the relentless pace of human activities, the dependence of system function and resilience on the number and characteristics of species present becomes an issue of considerable concern (Covich et al. 2004; Reid et al. 2019; Strayer and Dudgeon 2010).

12.2.1 Biodiversity and Ecosystem Function

The expectations that biodiversity matters to ecosystem function and also that high biodiversity serves as a buffer against the consequences of species loss have theoretical and empirical support (Loreau et al. 2002). Much of this work has been conducted in terrestrial ecosystems characterized

by relatively low levels of diversity (Lecerf and Richardson 2010). Several mechanisms potentially are responsible for relationships between biodiversity and ecosystem function (Giller et al. 2004). When species have complementary (overlapping but not identical) roles, the rate and efficiency of a process should increase when multiple species are present, and especially whenever the activities of one species facilitate those of a second. Thus, any species loss is expected to lower the efficiency of the process in question. When species have redundant roles, the loss of one species may not immediately result in a decline in the rate or efficiency of some process, and the presence of multiple, ecologically similar species provides insurance against a breakdown in ecosystem function should one or more species be adversely affected by environmental change (Toussaint et al. 2016).

Much of the work devoted to understanding biodiversity-ecosystem function relationships has been done in the context of trying to predict functional changes in rivers and streams as native biodiversity is lost from systems. In a review, Vaughn (2010) summarizes some of the primary conclusions that have emerged. First, the assemblage of species traits within a community mediates ecosystem processes through a combination of overlapping and non-overlapping roles. Additionally, taxa that are classified in the same functional group are not always ecologically equivalent, meaning their contribution to ecosystem processes may differ. A decline in the abundance of a common species is comparable to species loss, as a species does not have to be extirpated from a system to lose its functional role in ecosystem processes. Research in biodiversity-ecosystem function relationships in freshwater systems has also emphasized that losses to native biodiversity can affect an entire food web, and that the net effects of biodiversity loss are also dependent on the environmental context and change with shifting spatial and temporal scales. Long-term research is essential to understand how environmental conditions influence the effects of biodiversity on ecosystem processes, and lab and field manipulations allow researchers to control for environmental variables and track energy and nutrients as they move between organisms and the environment. (Vaughn 2010).

Leaf litter breakdown, discussed in detail in Chap. 7, provides evidence that this important ecosystem function is influenced by both species richness and species identity (Kominoski et al. 2010). Using laboratory microcosms, Jonsson and Malmqvist (2000) demonstrated that leaf mass loss increased with number of shredder species present, due either to differences in mode of feeding, facilitation of feeding efficiency, or both. By assembling a dataset of litter breakdown studies from 36 streams of northern Sweden and northeastern France, Dangles and Malmqvist (2004) were able to evaluate the influence of species richness versus

relative abundance components of diversity. The litter decomposition rate increased with the number of species present, but at a lower rate at sites with low dominance. In other words, detrital processing was more rapid in streams that were strongly dominated by one or a few species. Other studies have shown that the presence or absence of a single species, *Gammarus fossorum*, has a disproportionately strong influence on litter breakdown, and it is noteworthy that the highest breakdown rate occurred in a stream where this amphipod was the sole shredder present.

The effects of biodiversity on ecosystem processes can be more pronounced in systems characterized by low diversity, as redundancy in the functional capabilities of taxa may be limited. In a study of 24 high altitude (3200–3900 m), low diversity streams in the tropics, Dangles et al. (2011) employed in-situ experiments and observational data with modelling to assess the influence of shredder diversity on decomposition. They found that decomposition rates were best predicted by a linear model that described rates of decomposition as a function of both the relative abundance of the most effective shredders and increasing shredder diversity. When their approach was tested with datasets from 49 French and Swedish streams with more complex shredder diversity, the effects of richness and identity observed in less diverse systems were lost as the shredder community became more complex.

In contrast to the demonstrated influence of shredder diversity on leaf breakdown, fungal diversity apparently had no effect of leaf mass loss or fungal spore production (a measure of microbial production) in stream microcosms (Dang et al. 2005). This was true with oak and alder leaves, at high and low nutrient levels, and across a range of from one to eight fungal species. There was some suggestion of greater variability in fungal activity at low fungal diversity, consistent with a portfolio effect (the averaging and dampening out of the influence of extreme species as richness increases, just as a diverse stock portfolio is expected to guard against swings in a single stock's value). Although Bärlocher and Corkum (2003) reported a positive effect of fungal diversity on leaf decomposition rates, their result is less convincing because those authors relied on initial inoculates rather than realized communities, which typically have greater unevenness.

The particular suite of traits and functional roles of each species must be carefully considered, as individual species can have unique roles in ecosystems, be disproportionately abundant, dominate energy fluxes, and strongly influence other members of the assemblage. In some instances, individual species have been shown to play such a strong and unique role that species identity rather than overall diversity is of primary importance. This raises the possibility that a positive relationship between biodiversity and ecosystem function may be an artifact of sampling, because these

species with unique traits and roles are more likely to be encountered when more of the species pool is included in an experimental study.

If species loss is expected to result in reductions in ecosystem function, then highly diverse communities should be better buffered by their presumed greater levels of complementarity and redundancy, and therefore less affected by the loss of a single species (McIntyre et al. 2007). However, this is not always the case, as evidenced by a particularly striking example of a single species having substantial effects on ecosystem structure and function in a hyperdiverse tropical stream. During the dry season, the flannel-mouth characin *Prochilodus mariae* migrates from floodplain locations into headwater streams in the foothills of the Venezuelan Andes, where it feeds on organic-rich sediments on the streambed, creating visible feeding scars and enhancing sediment transport. *Prochilodus* is an ecosystem engineer, a species that significantly modifies habitat, often influencing habitat heterogeneity and species diversity. Comparisons between open and *Prochilodus*-restricted stream sections (Fig. 12.11) convincingly demonstrated that this one species of detritus-feeding fish uniquely influences carbon flow and ecosystem metabolism (Taylor et al. 2006). In its absence, the amount of particulate organic carbon on the stream bed was higher, the downstream flux of POC declined due to reduced bioturbation and consumption, heterotrophic respiration increased due to greater biofilm growth, and primary production doubled. Because respiration increased more than primary production, net ecosystem metabolism showed a greater deficit. This example is of more than academic interest: fishes of the Prochilodontidae are the most important commercial species of South America and are declining due to the combined influence of dams and over-fishing. Changes to ecosystem function seem all too likely to occur over large areas of the Neotropics due to the loss of species in this family.

12.2.2 Temporal and Spatial Variation in Ecosystem-Level Effects

The relationship between biodiversity and ecosystem function is influenced by changes in community composition and species interactions that vary with both biotic and abiotic conditions (Cardinale and Palmer 2002). Habitat heterogeneity affects ecosystem-level dynamics by influencing how organisms experience environmental conditions and by mediating the colonization and persistence of populations. By varying the size of streambed sediments in riffles while keeping the median substrate size constant, Cardinale et al. (2002) showed that increased heterogeneity in the physical habitat had immediate, stimulatory effects on primary productivity and respiration in benthic communities.

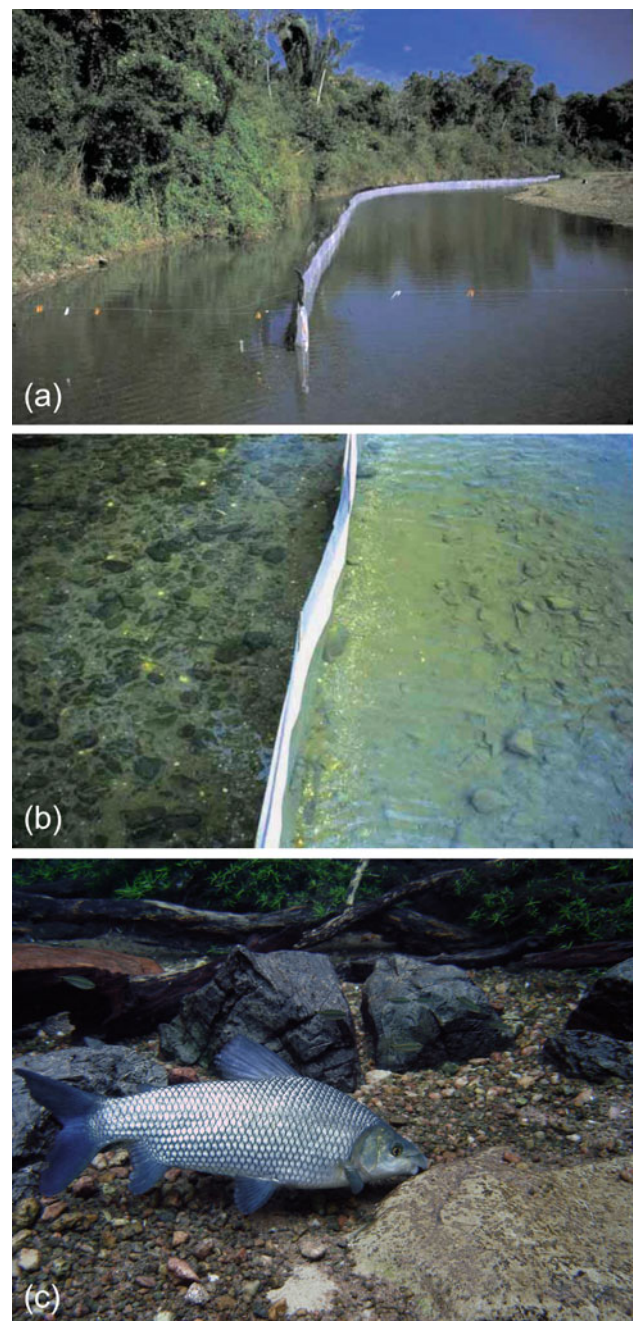


Fig. 12.11 Images of the *Prochilodus mariae* removal experiment. (a) The plastic divider in a 210 m section of Rio Las Marias in Venezuela. (b) Benthic particulate matter after removing *P. mariae* on the right compared with the intact fish assemblage on the left. (Reproduced from Taylor et al. 2006). (c) *Prochilodus* feeding on benthic sediments in the Prata river in the region of Bonito, Mato Grosso do Sul, Brazil. Photo courtesy of Ana Carolina O. Neves

Responses were attributed to changes in near-bed flow velocity and turbulence, suggesting disturbance regime may alter ecosystem processes.

Environmental variables, geographic location, and isolation all have been shown to affect biodiversity-ecosystem

function relationships. In watersheds that have limited connectivity to other freshwater systems, fewer species are available to colonize habitats and contribute to leaf litter processing. Pacific island streams in Micronesia have exceptionally low insect species richness and density, a complete absence of Ephemeroptera, Trichoptera, and Plecoptera, and an insect community dominated (~85% biomass) by non-shredding Chironomidae larvae (Benstead et al. 2009). In contrast to many streams in the temperate zone, macroconsumers, including decapods and gastropods, dominate this invertebrate community. Exclusion of macroconsumers by means of experimental electrified quadrats demonstrated that in streams of this region, microbes, rather than invertebrates, were primarily responsible for leaf-litter breakdown (Benstead et al. 2009).

Throughout the world, rivers and streams experience pronounced wet and dry seasons, and this can alter the net effects of species assemblages on productivity, respiration, and nutrient dynamics (Niu and Dudgeon 2011). Flashy, high flows can result in scouring of the benthos, removing primary producers, other microbes, and higher order consumers. Unless organismal biomass increases with increasing discharge, more frequent high flow events are likely to reduce the net influence of consumers on system-wide nutrient dynamics. Additionally, higher flows are typically correlated with more overland flow and more carbon and nutrients washing into streams. This may alter nutrient and carbon availability in river networks and cause changes in biogeochemical cycling. Seasonality is often linked to changing discharge, which can physically and chemically alter stream habitats and can also be linked to changes in community composition as certain species migrate in and out of a given reach.

Anthropogenic activities also may generate changes in species composition that subsequently alter ecosystem processes. For instance, microplastics are now commonly found in freshwater systems (Hoellein et al. 2014, 2017), and create new substrate for biofilm colonization. Though results are just beginning to emerge, studies suggest that biofilms colonizing microplastics are distinct from communities found in the surrounding environment. Using experimental manipulations and high-throughput sequencing of 16S rRNA to examine diversity patterns on biofilm communities on microplastics, Miao et al. (2019) observed that species richness, evenness, and diversity were lower in communities associated with microplastics than on natural substrates. Other research has found that the metabolic pathways of biofilm communities were distinct from those found on natural substrates, suggesting that changes in microbial diversity due to microplastic pollution may result in changes in microbially-mediated ecosystem processes (Abhauer et al. 2015).

Neotropical streams have lost many of their amphibian species due to the spread of a parasitic fungus, *Batrachochytrium dendrobatidis* (Bd), and this has subsequently altered ecosystem function in affected streams (Rantala et al. 2015; Whiles et al. 2013). To assess the impacts of the loss of tadpoles on leaf-litter decomposition in streams infected with Bd, Rugenski et al. (2012) evaluated the effects of grazing tadpoles, shredding macroinvertebrates, and both together on leaf decomposition and the associated microbial activity. Microbial respiration rates were greatest in treatments with tadpoles, indicating that grazing and nutrient mineralization by tadpoles enhanced microbial activity. Decomposition, measured by leaf area loss, was greatest in treatments with both tadpoles and macroinvertebrates, suggesting tadpole grazing facilitated invertebrate leaf processing by enhancing microbial production (Fig. 12.12). These results indicate that the presence of tadpoles benefits both microbial biofilms and shredding macroinvertebrates, and all play a functional role in the decomposition and generation of POM in these Neotropical headwater streams.

12.2.3 Community-Driven Nutrient Dynamics

The contribution of animals in mediating nutrient cycling, or consumer-driven nutrient dynamics (CND), influences stream ecosystem structure and function, with effects that vary among species and across ecosystems (Atkinson et al. 2017; Vanni 2002; Vanni et al. 2002). Through their consumption and storage of resources in body tissues, and subsequent mineralization of elements by excretion, egestion, and death and decomposition, consumers have the potential to regulate the flux of limiting nutrients, such as nitrogen and phosphorus, in lotic systems (Capps et al. 2015a). Hence, changes in community composition may alter freshwater food webs, as mineralization by consumers is expected to stimulate primary and secondary production, especially in nutrient limited systems (Vaughn 2010; Flecker et al. 2010). Two conceptual frameworks, ecological stoichiometry and the metabolic theory of ecology, help us understand the relative contribution of species to system-wide biogeochemistry through CND.

Ecological stoichiometry (Sterner and Elser 2002) is the study of the balance of elements in ecological processes, linking the body elemental composition of an organism to the resources it consumes and to the waste it produces through excretion, egestion, and decomposition. Because an organism must consume enough of each element that it requires to grow, any element in short supply relative to others (i.e., a limiting nutrient) will be preferentially retained by the organism and not released as waste. Put colloquially, if you eat it and need it, you should not excrete it. Ecological

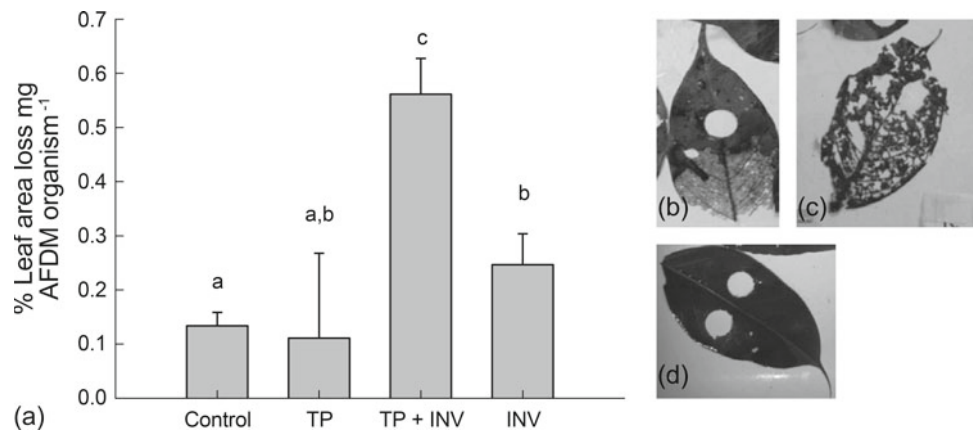


Fig. 12.12 Differences in leaf-litter decomposition rates among experimental treatments in chambers with no decomposers (control), tadpoles only (TP), tadpoles and macroinvertebrate shredders (TP + INV), and macroinvertebrates only (INV). (a) Average ($\pm 1SD$) amount (%) of leaf area lost per unit detritivore (i.e., tadpoles and macroinvertebrates) biomass after 31-day incubations. Photographs of examples of leaves (b) with tadpoles only (TP), (c) tadpoles and

invertebrate shredders (TP + INV) and (d) macroinvertebrates only (INV). The circles within the leaves in each of the photographs were sections of the leaves removed to estimate microbial respiration. The different letters in (a) reflect significant differences between treatments ($\alpha = 0.05$; one-way analysis of variance and Tukey's multiple comparisons). (Reproduced from Rugenski et al. 2012)

stoichiometry largely rests on what is known as the Law of the Minimum, developed in the mid-nineteenth century, which states that whatever element is in least supply in the environment relative to an organism's needs will limit its growth. Interest in stoichiometric applications grew with the observation that the ratio of carbon to nitrogen to phosphorus in marine phytoplankton is a relatively constant 106:16:1 and similar to dissolved nutrient pools in sea water (Redfield 1958), and with further studies of the elemental mass balance of aquatic organisms (Corner et al. 1976). These early studies set the stage for research into the influence of CND on food web ecology and biogeochemistry (Hessen et al. 2013).

The metabolic theory of ecology (Brown et al. 2004) outlines a theoretical basis for linking first principles of biology, chemistry, and physics to how organisms interact with their environment. Specifically, this theory explores how metabolic rate can be quantitatively linked to body size and temperature. The rates at which an organism uses resources within the environment, and how these resources are allocated to survival, growth, and reproduction, govern ecological processes including but not limited to, the rate of development, population growth rate, species interactions, and system-wide productivity and respiration rates.

When considered together, ecological stoichiometry and the metabolic theory of ecology suggest that nutrient mineralization by animals (i.e., excretion, egestion, and tissue decomposition) should depend on the expression of certain species traits, especially body size, trophic ecology, and ontogeny (Vanni and McIntyre 2016; Atkinson et al. 2017). For instance, amphibians experience large shifts in the ratio of carbon, nitrogen, and phosphorus in their tissues as they

develop from cartilage-based larvae into juvenile animals with boney skeletons, a phosphorus-rich tissue (Tiegs et al. 2016; Luhring et al. 2017).

Variation in growth or ingestion among individuals may reflect different patterns in nutrient limitation among organisms and across systems, and this may shift relationships between the stoichiometry of body tissues and the stoichiometry of waste released by an animal (Vanni and McIntyre 2016). If growth rates among or within taxa are not strongly nutrient-dependent, and species are not consistently growing or building new tissues through their lifetime, body stoichiometry may influence excretion stoichiometry, and animals as could release wastes at the same N:P ratio as consumed in their food. However, when a nutrient is in high demand for building tissue and in short supply in the animal's diet, as for example P required for bone elaboration, the ratio of nutrients in excretion can indicate selective retention of a limiting nutrient.

Variation in ingestion rates can also produce relationships contrary to the predictions of ecological stoichiometry, as animals frequently compensate for low-quality diets by consuming more food (Bowen et al. 1995). Hence, the net intake of nutrients by a consumer may be regulated by the quantity rather than the nutritional value of their food. Animal growth is often limited by carbon or energy rather than by nutrients such as phosphorus (Schindler and Eby 1997; Frost et al. 2006), though phosphorus limitation may occur in primary consumers with low phosphorus diets (Sturner 1990; Hood et al. 2005; Benstead et al. 2014). Animals that are limited by energy may consume, and subsequently excrete or egest, excess nutrients in order to acquire enough energy for growth or reproduction,

decoupling the relationship between the chemical composition of body tissues and their waste (Vanni and McIntyre 2016; Vanni et al. 2017).

The net contribution of a population or community of organisms to system-wide biogeochemistry depends on their abundance, the rates at which they store and mineralize nutrients, and the physicochemical conditions of the environment, including discharge and ambient nutrient concentrations (McIntyre et al. 2008). For example, Wheeler et al. (2015) and Atkinson and Vaughn (2015) assessed the effects of stream discharge on the roles of fish and mussel excretion on ecosystem processes in streams, respectively. As water volumes declined in drier weather, the ratio of organismal biomass to discharge increased, as did the relative contribution of organism to system-wide nutrient dynamics. Ambient nutrient concentrations can also influence how consumers contribute to nutrient dynamics. In streams along an agricultural gradient, Wilson and Xenopoulos (2011) demonstrated that excretion of nitrogen and phosphorus by fishes was able to fulfill more of the ecosystem-level demand for both elements as the amount of cropland increased. This was especially notable because ambient nutrient concentrations also increased along this gradient, attributed to increases in fish biomass concurrent with increasing ambient nutrient concentrations. In contrast, increasing ambient nutrient concentrations along an agricultural gradient catchment all but eliminated the contribution of mussels to system-wide biogeochemical cycling (Spooner et al. 2013). This work demonstrated that while species can persist in anthropogenically-disturbed environments, their functional roles in ecosystem-level processes may be compromised.

Drought is both a natural and an anthropogenically-mediated disturbance that affects ecosystem processes by altering freshwater community structure. Mussels dominate biomass in some freshwater systems, and although their distribution can be patchy, they can be important contributors to nutrient storage and cycling (Vaughn et al. 2015). Of all groups of freshwater organisms, mussels are often of greatest conservation concern, as many species are exceptionally sensitive to environmental change (Vaughn 2010). In a survey of mussel populations at nine sites within three rivers in the south-central US before and after an exceptional regional drought, Atkinson et al. (2014) documented changes in nutrient storage and mineralization in response to declines in mussel density and biomass. Mussel die-off reduced nitrogen concentrations in the water column and reduced phosphorus storage in mussel tissue, potentially influencing system-wide nutrient dynamics (Fig. 12.13).

As previously discussed, animals can transport elements across habitat boundaries, generating spatial subsidies in

rivers and streams. Childress and McIntyre (2015) showed that longnose suckers *Catostomus catostomus* transported elements from the Laurentian Great lakes into tributary streams via excretion and egg deposition (Fig. 12.14), and excretion had large effects on nutrient inputs even in streams influenced by agriculture. Similarly, Subalusky et al. (2015) coupled empirical measurements collected at a zoological park with observed hippopotami (*Hippopotamus amphibius*) densities in the Maasai Mara National Reserve in Kenya to estimate that hippos in the watershed could contribute large proportions of the Mara River's coarse particulate organic matter, total nitrogen, and total phosphorus relative to nutrient loading from the upstream catchment (Fig. 12.15).

Animals often aggregate in space (e.g., mussel beds) and time (e.g., diurnal pool use by hippos), and this can influence when and where they consume and mineralize resources, and thus the heterogeneity of biogeochemical cycling in rivers and streams. In a study of the fish community of a diverse, nitrogen-limited stream in Venezuela, McIntyre et al. (2008) measured the nitrogen and phosphorus excretion rates and population densities of approximately 50 species of fishes. Although excretion rates of both elements varied considerably among species of fishes, collectively the excretion by the fish community could meet more than 75% of the ecosystem demand for dissolved inorganic nitrogen at the reach scale. Fish population densities differed sufficiently among riffles, runs, and pools such that, when controlled for size of the habitat, there was a 47-fold difference in nitrogen excretion and a 14-fold difference in phosphorus excretion among habitat units, suggesting that fishes may be creating hotspots of biogeochemical activity in this system. The introduction of a novel species also may have demonstrable effects on ecosystem processes. In river systems in southern Mexico, diel aggregations of the non-native catfish (Loricariidae: *Pterygoplichthys*; Fig. 12.16), a nocturnal feeder, generated measurable changes in nitrogen and phosphorus dynamics in a nutrient-limited river (Capps and Flecker 2013a, b).

Though not extensively studied, the influence of parasites and disease in freshwater communities may also generate variability in the contribution of organisms to ecosystem function by changing consumer metabolism and behavior. In a study of the elemental content of trematodes and their gastropod hosts, Bernot (2013) found a mismatch of the ratio of nitrogen to phosphorus in the parasite and in most gastropod tissues. Additionally, nutrient mineralization ratios in snails infected by trematodes differed from uninfected snails. Much more remains to be learned about these interactions, but this study suggests that parasite infection should be considered when examining the functional contribution of species to ecosystem-level processes.

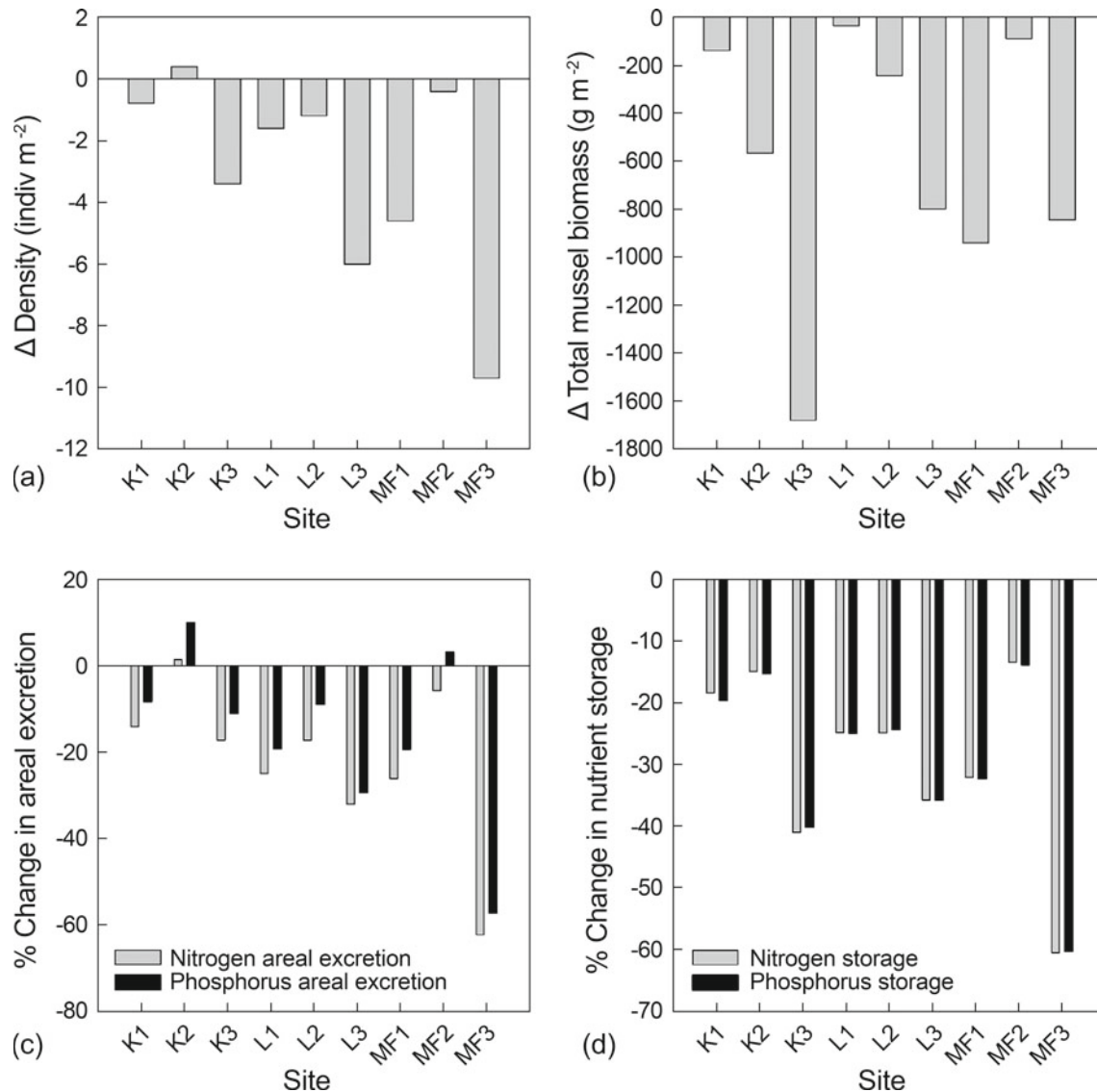


Fig. 12.13 Changes in the density (a) and total biomass (dry tissue + shell biomass) (b) of freshwater mussels in streams in the south-central US observed in 2010 (pre-drought) and 2012 (post-drought) conditions. The percent change in areal nitrogen and

phosphorus (c) excretion rates and (d) storage in living mussel tissues between the two time periods also is shown. (Reproduced from Atkinson et al. 2014)

12.3 Summary

Species within aquatic communities play essential roles in system-wide energy and nutrient dynamics, connecting the biotic with the abiotic components of rivers and streams. The network of interactions portrayed in a food web provides the most complete yet succinct visual summary of a biological community. Identification of all links, although rarely achieved, serves as a useful reminder of the potential complexity within biological communities. Most energy flows through a subset of species, and typically it is the common species that dominate energy pathways.

Spatial subsidies occur when nutrients and energy flow across habitat boundaries, often with profound influence on recipient ecosystems. These subsidies are diverse across seasons and systems, and include allochthonous litter inputs, the exchange of invertebrates between the stream ecosystem and the terrestrial riparian zone, and upstream–downstream transfers due to water flows, animal migrations, and anthropogenic inputs. Differences in productivity and characteristics of the boundary between donor and recipient systems influence the lability, quantity, timing, and duration of a subsidy entering the new system; thus, the network of interacting species within stream ecosystems is strongly influenced by landscape setting.

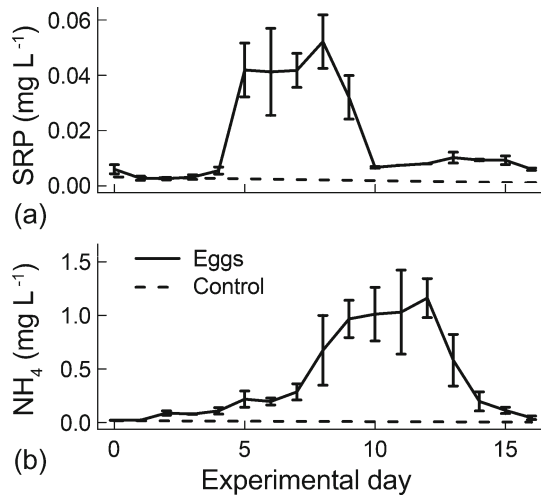
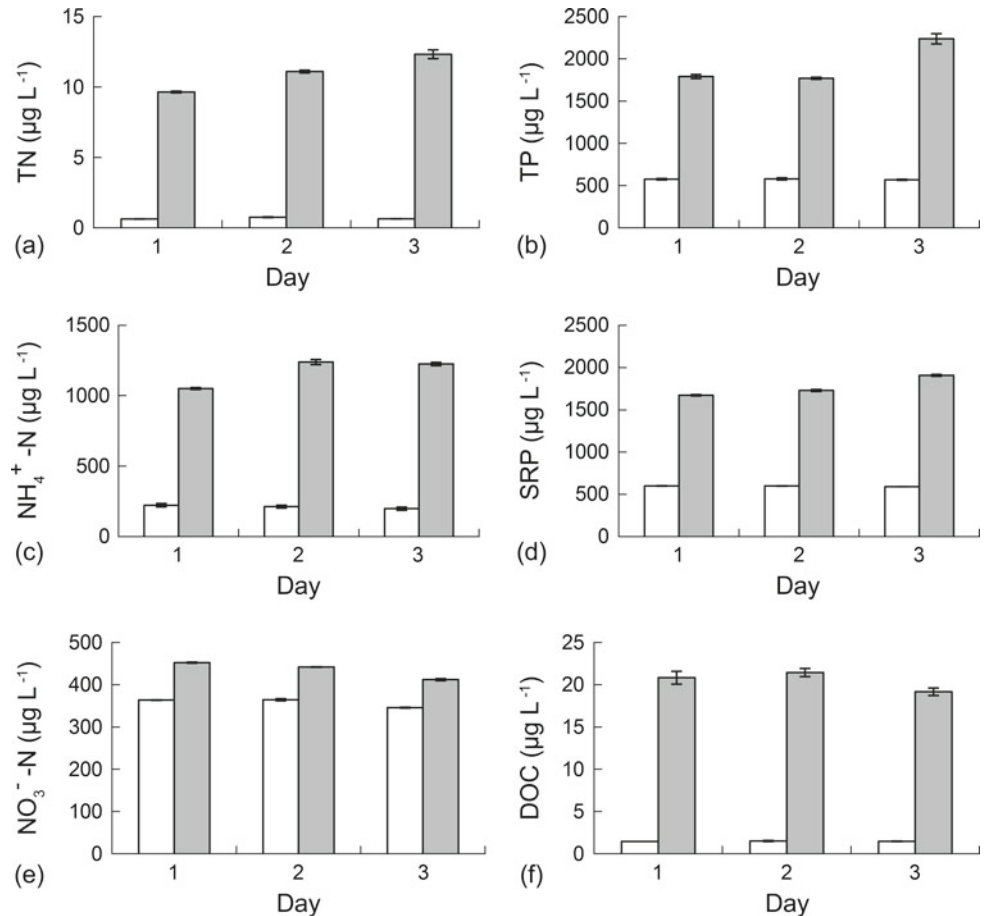


Fig. 12.14 Changes in ambient nutrient concentrations in microcosms through the decomposition of sucker eggs in microcosms with and without eggs: (a) soluble reactive phosphorus (SRP), and (b) ammonium (NH₄⁺). (Reproduced from Childress and McIntyre 2015)

Fig. 12.15 Nutrient and carbon concentrations in a habitat pool for hippopotamus at the Milwaukee County Zoo before (white) and after (grey) approximately one day of use by three adult hippopotami. The bars are ± 1 standard error. (a) total nitrogen (TN), (b) total phosphorus (TP), (c) ammonium-nitrogen (NH₄⁺-N), (d) soluble reactive phosphorus (SRP), (e) nitrate-nitrogen (NO₃⁻-N), (f) dissolved organic carbon (DOC). (Reproduced from Subaluský et al. 2015)



Community structure refers to the organization of a biological assemblage based on numbers of individuals within different taxonomic groups and functional roles, and the underlying processes that maintain that organization. Functional classifications can be based on a variety of species attributes, including but not limited to, ecosystem engineering, feeding ecology, productivity, and the capacity for elemental mineralization.

Ecosystem function relies on the presence of multiple species. Species performing complementary roles should increase the rate and efficiency of a process, and redundancy in the functional role of species increases the resilience of an ecosystem, ensuring that the loss of one species may not immediately result in a decline in the rate or efficiency of some process. Studies have revealed that one or a few species can be especially strong interactors in an ecosystem process, such that the loss of a single species can profoundly alter ecosystem function.

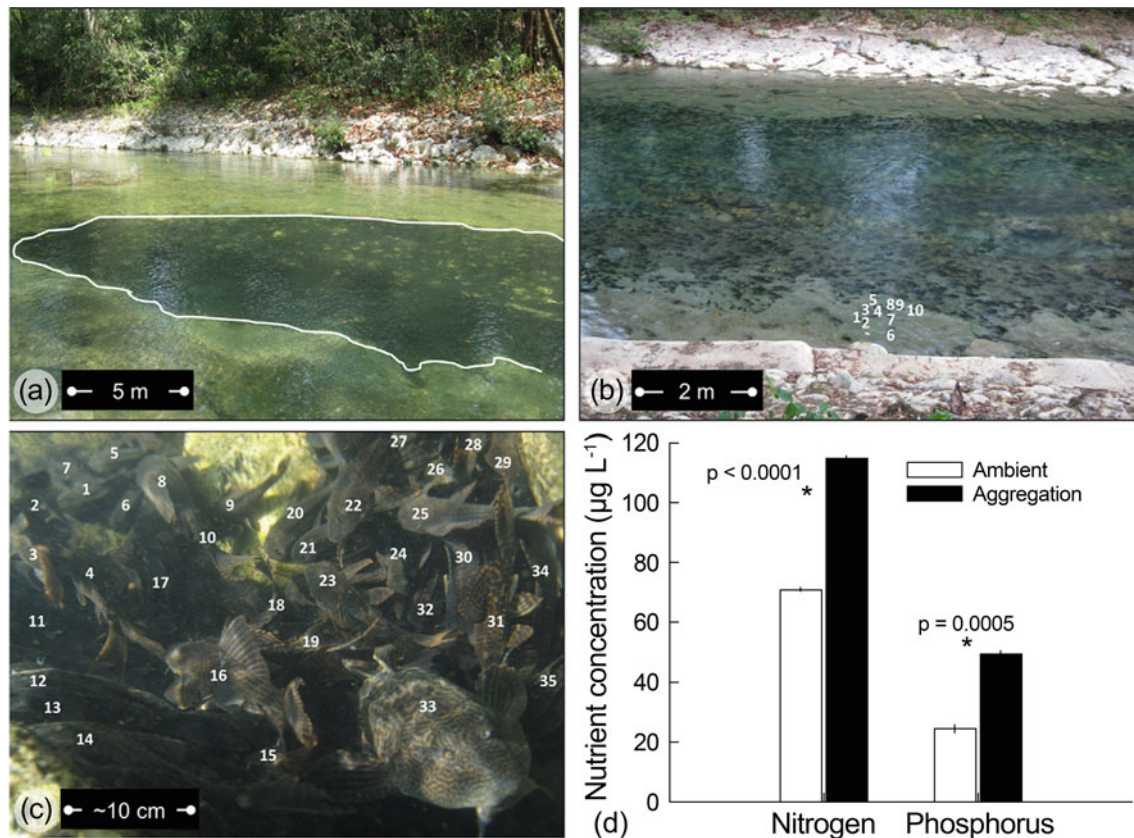


Fig. 12.16 Invasive armored catfish (*Pterygoplichthys*) in southern Mexico. (a) Daytime aggregation of catfish outlined by the white line. (b) Fish leaving the aggregation at dusk. Each dark spot is at least one fish and a small group of fishes (1–10) has been marked with individual numbers to emphasize the abundance of the catfish. (c) Underwater image of aggregation where individual fish are marked with white numbers (1–35). (d) Mean values (± 1 SE) of nitrogen (N; $\text{NH}_4^+\text{-N}$) and

phosphorus (P; $\text{PO}_4^{3-}\text{-P}$) collected from paired sites within and outside of catfish aggregations. Aggregations were defined as groups of *Pterygoplichthys* that had an area of at least five square meters with at least 40 *Pterygoplichthys* per m^2 . Ambient samples were collected from sites parallel to the aggregations without immediate upstream aggregations of the fish. (Reproduced from Capps and Flecker 2013b)

Animals can play a critical role in biogeochemical cycling, referred to as consumer-driven nutrient dynamics. Animals consume and store resources in body tissues, and subsequently mineralize elements through excretion, egestion, and death and decomposition. Spatial and temporal variation in resource and habitat availability and the distribution and activity of species within systems can create hotspots of biogeochemical processes, including biological production, respiration, and nutrient mineralization. The loss of species due to human activities is an increasingly serious concern, and raises the possibility that simplified communities may become less productive and less resilient.

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