9

Trophic Relationships

The network of consumers and resources that comprise fluvial food webs is supported by a diverse mix of energy supplies that originate within the stream and beyond its banks. These include the living resources of algae and higher plants, and the non-living resources of particulate and dissolved organic matter, especially material derived from dead and decaying plant matter. Microorganisms are important mediators of organic matter availability, and there is increasing evidence of their importance as a resource to both small and large consumers. Additionally, energy subsidies in the form of falling terrestrial arthropods and the eggs and carcasses of migrating fish contribute to the support of many stream-dwellers. Energy sources within a stream reach are not necessarily consumed within that part of the stream, as downstream export, insect emergence, and fish movements can supply energy to distant ecosystems.

Trophic organization in river ecosystems can be complex and indistinct. Many consumers are polyphagous rather than monophagous, and exhibit considerable overlap with one another in their diets. The gut contents of invertebrates can be difficult to identify with great confidence, so these consumers often are characterized by the unspecific term of herbivore-detritivore. In many systems, especially those in the temperate zone, the vast majority of fishes eat invertebrates. As a consequence, while a particular species may be classified solely on the basis of what it eats—herbivore, predator, detritivore, and so on—the resulting categories can be of limited usefulness because they offer too few distinctions among feeding roles. Further resolution of trophic status can be achieved by distinguishing among feeding roles on the basis of how the food is obtained, rather than solely in terms of what food is eaten, and by consideration of morphological adaptations for food capture.

When several species consume a common resource and acquire it in similar fashion, they are considered members of the same feeding group, commonly referred to as a trophic category or guild. Thus, a fish species that captures invertebrate prey directly from the bottom would occupy a different trophic category from another species that consumes the same prey, but captures them from the water column. Invertebrates typically are divided into functional feeding groups on the basis of resource category, where or how the resource is obtained, and morphological adaptations for food capture (Cummins 1973). It is important to note that members of different invertebrate functional groups may consume the same resource: for example, fine particulate organic matter can be captured from the water column or collected from depositional areas within a stream. Hence, the main difference between consumers is not the resource, but the organism's method of acquiring it. Compared to macroinvertebrate classifications, fish trophic categories often rely primarily on what resources is consumed, but also may consider feeding location and morphology.

Traditional methods for investigating the feeding roles of invertebrate species include gut-content analysis, fecal analysis, and behavioral observations. Such studies can provide detailed information on primary feeding mode for many if not most species, and have long been long been the basis for trophic classification. In addition, studies of feeding can be complemented with morphological analysis of feeding mechanism, chemical analyses of resource and consumer tissue, and experimental studies (Gelwick and McIntyre 2017). Recent years have seen broader use of powerful new tools that provide fresh insight into the energy sources that consumers assimilate into their tissue (Post 2002; Finlay et al. 2010). In many instances, studies provide evidence that less abundant food sources actually contribute disproportionately to consumer energy intake: in other words, what consumers eat and what they assimilate can be quite different. Stable isotopes of C, N, and H are becoming widely used as food web tracers in aquatic ecosystems, because isotopic ratios of consumer proteins reflect the proteins of their food sources, and some isotopic ratios change with each trophic transfer. The ratio of carbon isotopes ($^{13}C/^{12}C$ abbreviated as $\delta^{13}C$) relies on isotopic differences between algae and plant matter of terrestrial origin. Algae generally

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have a higher $^{13}C/^{12}C$ ratio (are "enriched" in ^{13}C) relative to terrestrially-derived C, although variability among algal taxa associated with environmental conditions, including water velocity, may limit insights from this tracer alone (Finlay et al. 2010). The isotopes of nitrogen are most useful for estimating trophic position because the ratio ($^{15}N/^{14}N$ abbreviated as $\delta^{15}N$) of a consumer is typically enriched by 3–4% relative to its diet. In contrast, the $\delta\,^{13}C$ changes little as carbon moves through food webs, allowing it to be used to evaluate the ultimate sources of carbon for an organism when the isotopic signature of the sources are different. The stable isotope of hydrogen ($\delta\,^{2}H$, or δD for Deuterium) can be used to evaluate allochthony in aquatic systems because terrestrially-derived resources in streams are substantially enriched in $\delta^{2}H$ relative to autochthonous material (Doucett et al. 2007). Many animal consumers are dependent on their food supply to obtain lipids important to their growth. Certain fatty acids are biomarkers for cyanobacteria and diatoms, while others are more characteristic of allochthonous resources, and so can distinguish the relative importance of autochthony versus allochthony to consumer assimilation. Although not yet in wide use, recent development of microbial biomarkers holds promise for improved assessment of the microbial compartment of food webs (Middelburg 2014).

Historically the study of trophic relationships has emphasized the larger animal consumers, but a growing appreciation of the contribution of bacteria and fungi to the diet of macro-consumers, as well as the potential importance of protists, micro-metazoans, and early instars of macroinvertebrates in energy transfers, have led to a greater focus on the importance of microbial food webs. Biofilms in particular have been shown to be important energy complexes where algae and microorganisms living in close association are able to capitalize on the energy obtained from sunlight and from organic matter, and so autotrophic and heterotrophic pathways can be closely linked. The trophic ecology of micro-consumers and energy supplied through microbial production are explored in Chap. 8; in this chapter we focus on the macro-consumers groups of invertebrates, fishes, and other vertebrates.

9.1 Invertebrate Feeding Roles

Macroinvertebrates are major components of riverine food webs, serving as important links between basal resources and higher trophic levels. However, traditional categories of food consumption, such as herbivore, detritivore, predator, etc., are of limited use for stream invertebrates. Most aquatic invertebrates are omnivorous, at least in their early life stages, and many retain this flexibility throughout their lives. Accidental ingestion of diverse food items wherever detritus, algal films, and small invertebrates are intermixed, and the often amorphous nature of gut contents, further compounds the difficulty of portraying stream food webs. The establishment of functional feeding groups (FFGs, Cummins 1973; Cummins and Klug 1979), and their association with most North American taxa (Merritt et al. 2019), was a major advance that has found wide use in stream ecology.

Table 9.1 lists the main FFG categories, their dominant food, feeding mechanism, and typical size range of particles

Table 9.1 Functional feeding groups (FFGs) of aquatic invertebrates, based on Merritt et al. (2017, 2019). Categories and size ranges are generalizations, and main FFG categories can be further subdivided based on feeding mechanism

Functional feeding group	Dominant food	Feeding mechanism	General particle size range of food (mm)
Shredders	Decomposing vascular plant tissue (CPOM) Living vascular plant tissue Wood	Detritivores-chewers of CPOM Herbivore-chewers and miners of live macrophytes Borers and gougers	>1
Collectors	Decomposing FPOM and associated microflora and—microfauna	Detritivore-filterers (suspension feeders) Detritivore-gatherers (deposit feeders)	<1
Scrapers	Periphyton—attached algae and associated microflora and—microfauna	Herbivores scraping, grazing, and browsing on mineral and organic substrates	<1
Macrophyte piercers	Living vascular plant cell tissues and fluids	Herbivores pierce tissues and suck fluids	>1
Predators	Living animal tissue	Carnivores that ingest entire animal or parts Carnivores that pierce tissues and suck fluids	>1
Parasites	Living animal tissue	Internal and external parasites of all life stages	>1

consumed. Scrapers consume non-filamentous attached algae from substrates (coarse sediments, wood, or stems of rooted aquatic vascular plants). Detrital shredders primarily feed on leaves or needles of terrestrial plant litter (coarse particulate organic matter, CPOM) entrained in the stream and colonized by microbes. Gathering collectors have very generalized adaptations to feed on fine particulate organic matter (FPOM) from depositional areas or crevices. Filtering collectors capture FPOM in suspension in streams using morphological structures or silk capture nets. Herbivore shredders are adapted to feed on live rooted aquatic plants, primarily the leaves. Herbivore piercers are adapted to pierce individual filamentous algal cells and suck out the cell contents. Predators are adapted to catch and consume live prey by engulfing the prey or piercing and extracting the prey hemolymph.

Within a given FFG one finds different taxonomic groups and a variety of adaptations with regard to mouthparts and food-gathering mechanisms. Mouthparts adapted for scraping benthic algae from hard surfaces are broadly similar amongst caddis larvae from different families (Glossosomatidae, Helicopsychidae) and a beetle larvae (the water penny, Psephenidae). Similarly, the mandibles of three genera of wood gougers, including *Heteroplectron* (Trichoptera), *Lara* (Coleoptera), and *Lipsothrix* (Diptera) all have three teeth and are scoop-shaped with basal setae that aid in passage into the mouth of the removed wood fragments and contained microbes (Cummins 2018). Aquatic insects specialized for suspension feeding may have different morphologies that nonetheless filter small particles from the water column, such as setae along the forelegs of some mayfly nymphs, and the nets of hydropsychid caddis larvae.

The FFG system assumes a direct correspondence between basal resources available at a stream location and the populations of macroinvertebrates that are adapted to efficiently harvest those food resources (Merritt et al. 2017). Periphyton, coarse and fine particulate organic matter, and other animals are the main categories of basal resources, described in Chaps. 6 and 7 (although the biofilms discussed in Chap. 8, containing microbes, algae, and meiofauna, occur widely and complicate this neat partitioning). Differences in the size of the food items, such as CPOM vs FPOM; its location, either suspended or attached to or deposited on the stream bed; and whether or not resources are living or dead, are further correlates of FFG designation. Thus, the use of FFGs to characterize the macroinvertebrate assemblage at a stream location provides insight into functional roles, basal resource availability, and the importance of allochthony vs autochthony. In essence, functional feeding group classification tells us that shredders feed on CPOM, collectors feed on deposited (gatherers) and suspended (filterers) FPOM, scrapers consume periphyton, piercers feed on live algal cell contents in periphyton, and predators ingest prey. Parasites and pathogens seldom are considered explicitly, but have much in common with predators.

9.1.1 Consumers of CPOM

Figure 9.1 depicts the shredder:CPOM linkage typical of a small stream in the temperate zone. The consumption of autumn-shed leaves in woodland streams by the invertebrates termed shredders is the most extensively investigated trophic pathway involving CPOM (Cummins and Klug 1979), and shall serve as our model here. Invertebrates that feed on decaying leaves include crustaceans (especially amphipods, isopods, crayfish, and freshwater shrimp), snails, and several groups of insect larvae. The latter includes crane fly larvae (Tipulidae), and several families of the Trichoptera (Limnephilidae, Lepidostomatidae, Sericostomatidae, Oeconesidae), and Plecoptera (Peltoperlidae, Pteronarcidae, Nemouridae). The leaf-shredding activities of insect larvae and gammarid amphipods are particularly well studied (Table 9.2). *Tipula* and many limnephilid caddis larvae eat all parts of the leaf including mesophyll and venation, whereas peltoperlid stonefly nymphs avoid venation and concentrate mainly on mesophyll, cuticle, and epidermal cells (Ward and Woods 1986). The radula of snails and mouthparts of *Gammarus* are most effective at scraping softer tissues, and the bigger crustaceans are able to tear and engulf larger leaf fragments (Anderson and Sedell 1979). Different feeding modes among CPOM detritivores also have consequences for the production of FPOM. The caddis *Limnephilis* produced small particles at a higher rate than two crustacean shredders, and both the size fractions and C:N ratios of fine particles generated varied with the mix of detritivore species (Patrick 2013).

Selection of food by shredders is based on several characteristics of leaves such as toughness, nutrient content, the presence of plant chemical defenses, and the degree of conditioning by microorganisms (Graça 2001). The nutritional quality of leaves is intimately linked with the microorganisms that contribute so greatly to leaf breakdown. Much effort has been directed at determining how microorganisms directly (as food) and indirectly (by modifying the substrate) contribute to the nourishment of CPOM consumers, and what capabilities these detritivores possess to digest the various components of their diet. Invertebrate detritus-feeders unquestionably prefer leaves that have been “conditioned” by microbial colonization in comparison to uncolonized leaves. When presented with elm leaves that were either autoclaved or cultured with antibiotics to inhibit microbial growth, versus normal colonized leaves, *Gammarus* consumed far more of the latter (Kaushik and Hynes 1971). Subsequent work has confirmed that preference is greatest for leaves at the stage of conditioning that

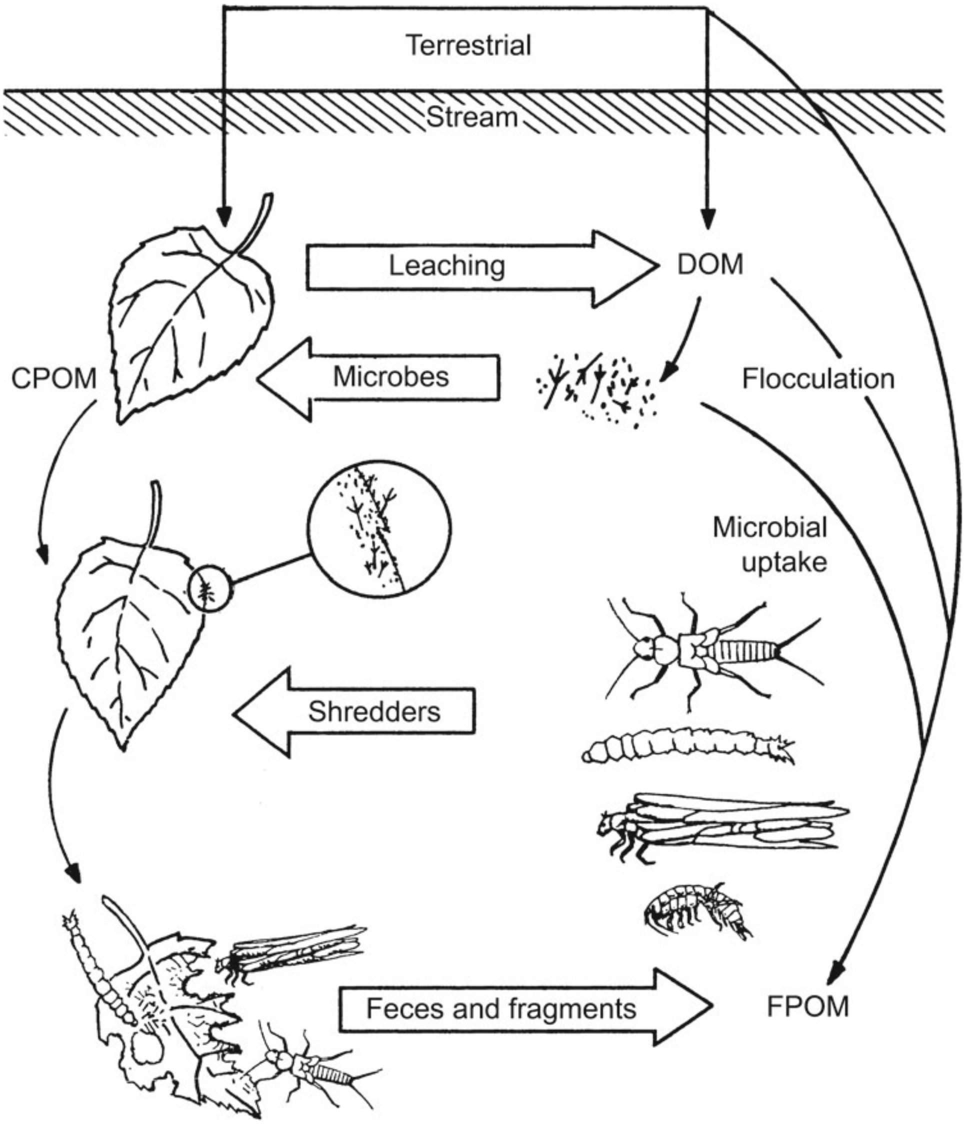

Fig. 9.1 The shredder:CPOM linkages for a small stream within a temperate deciduous forest. Physical abrasion, microbial activity (especially by fungi), and invertebrate shredders reduce much of the CPOM to smaller particles. Chemical leaching and microbial excretion and respiration release DOM and CO_2, but much of the original carbon enters other detrital pools as feces and fragmented material (Reproduced from Cummins and Klug 1979)

Table 9.2 The contrasting feeding strategies of two CPOM detritivores. Based on Barlöcher (1983)

	Gammarus fossarum	*Tipula abdominalis*
Feeding mechanism	Scrapes at leaf surface	Chews entire leaf
Gut pH and digestive biochemistry	Anterior gut slightly acid Its own enzymes and fungal exoenzymes attack leaf carbohydrates Posterior gut is alkaline, can digest microbial proteins and some leaf proteins	Foregut and midgut highly alkaline (up to 11.6) Results in high proteolic activity but inactivation of fungal exoenzymes, thus little activity toward leaf carbohydrates
Efficiency	Highly efficient at processing conditioned leaves at low metabolic cost	Less dependent upon stage of conditioning, probably good at extracting protein, but at high metabolic cost
Other attributes of feeding ecology	Highly mobile	Low mobility
	Polyphagous	Obligate detritivore

corresponds to the period of greatest microbial growth (Arsuffi and Suberkropp 1984; Suberkropp and Arsuffi 1984). The benefits to the consumer include greater efficiency in converting ingested leaf biomass into consumer biomass and a higher individual growth rate.

Preference trials that compared shredders from tropical and temperate locations provided with conditioned (leaves submerged in the stream for two weeks) and unconditioned leaves from a temperate and a tropical tree found that all shredders preferred conditioned over unconditioned leaves regardless of the region of origin of either the shredders or the leaves (Fig. 9.2). In addition, all grew faster when provided with the conditioned leaves (Graça 2001). Considering that the leaves of the temperate tree (alder, *Alnus glutinosa*) have been shown to be a preferred food in a number of studies, whereas the tropical tree (*Hura crepitans*, Euphorbiaceae) produces a milky juice used by Amerindians to make poison darts, a general preference for alder leaves is no surprise. More surprising is the observation that *Gammarus* showed no preference among conditioned leaves, and shredders grown on *Alnus* and *Hura* did not differ in survival and growth rates, indicating that leaf conditioning was more important than leaf type.

Green and senescent leaves differ in their phenol, lignin, and nutrient content, and thus in their quality as food. Larvae of the caddis *Lepidostoma complicatum* grew more slowly on green than senescent leaves and none reached maturity, whereas 70% of larvae fed senescent leaves reached the adult stage (Kochi and Kagaya 2005). However, larvae that were given both senescent and green leaves had a faster growth rate than those provided with senescent leaves only, probably due to the higher nitrogen content of green leaves. The freshwater shrimp *Xiphocaris elongate* was found to prefer leaves of *Dacryodes excelsa* over *Cecropia schebe-riana*, despite their higher secondary compound content and firmness, apparently because of the lower lignin content of *Dacryodes* leaves (Wright and Covich 2005).

Microorganisms may enhance the palatability and nutritional quality of leaves in at least two distinct ways (Barlöcher 1985). One, termed microbial production, refers to the addition of microbial tissue, substances, or excretions to the substrate. Because assimilation efficiencies on fungal mycelia and mixed microflora have been shown to exceed 60%, while values for conditioned and unconditioned leaves average near 20% (Martin and Kukor 1984; Barlöcher 1985), indications are that the nutrient content per unit mass in microorganisms can be several-fold greater than that of the leaf substrate. The second potential role for microorganisms is microbial catalysis, which encompasses all of the changes that render the leaf more digestible. This includes partial digestion of the substrate into sub-units that detritivores are capable of assimilating, and production of exoenzymes that remain active after ingestion. As support for this proposition, Barlöcher (1985) pointed out that structural carbohydrates (cellulose, hemicellulose, pectin) may be partially digested by microorganisms into intermediate products which the gut fluids of invertebrates are then able to degrade. Indeed, leaves subjected to partial hydrolysis with hot HCl were preferred by *Gammarus pseudolimnaeus* over untreated leaves (Barlöcher and Kendrick 1975). Barlöcher (1982) also showed that fungal exoenzymes extracted from decomposing leaves remained active in the presence of gut enzymes of *G. fossarum* for up to four hours at the foregut's pH, indicating that ingested exoenzymes can aid in the digestion of polysaccharides.

Some shredders may be able to actively discriminate between fungi and leaf material. In feeding trials with the freshwater detritivores *Gammarus. pulex* and *Asellus aquaticus*, Graca et al. (1993) found that both species discriminated between fungal mycelia, fungally colonized leaf material, and uncolonized leaf material. Individuals of *A. aquaticus* selectively consumed fungal mycelia whereas *G. pulex* fed preferentially on leaf material, and for the latter species fungi appeared to be more important as modifiers of leaf material. Using radio-labelled food sources and inhibitors of DNA synthesis, Findlay et al. (1984, 1986) demonstrated that only 15% of the respired carbon in the freshwater isopod *Lirceus* and 25% in the stonefly *Peltoperla* was met by consumption of microbes, primarily fungi. In addition, while insect larvae may lack the ability to synthesize cellulolytic enzymes, Sinsabaugh et al. (1985) demonstrated using radio-labelled cellulose substrate that leaf-shredding insects indeed were able to digest and assimilate plant cell wall polysaccharides. The authors inferred that digestion was aided by ingested exoenzymes in the case of *Pteronarcys*, and by endosymbionts in the distinctive rectal lobe of the hindgut of *Tipula*. Leaf-shredding crustaceans produce enzymes that enhance their ability to digest leaf litter of terrestrial origin. The amphipod *G. pulex* produces phenol oxidase and cellulase activity in the hepatopancreas, whereas in the isopod *A. aquaticus* these enzymes are produced by endosymbiotic bacteria (Zimmer and Bartholmé 2003).

Algae and bacteria of biofilms associated with leaf litter may contribute substantially to shredder nutrition. The exclusion of leaf litter from experimental stream reaches forced greater reliance on biofilms, and the shredders *Tallaperla* and *Tipula* derived on average 32 and 14% of their carbon from bacteria respectively, probably in the form of bacterial exopolimers (Hall and Meyer 1998). Shredders can also obtain carbon from algae growing on leaf biofilms, where the algae can increase the food quality of leaf biofilms and also stimulate microbial production by the release of exudates, and thereby enhance the growth of shredders (Franken et al. 2005). Algae attached to leaf litter may also influence the fatty acid composition of shredder diet, and thereby enhance shredder growth.

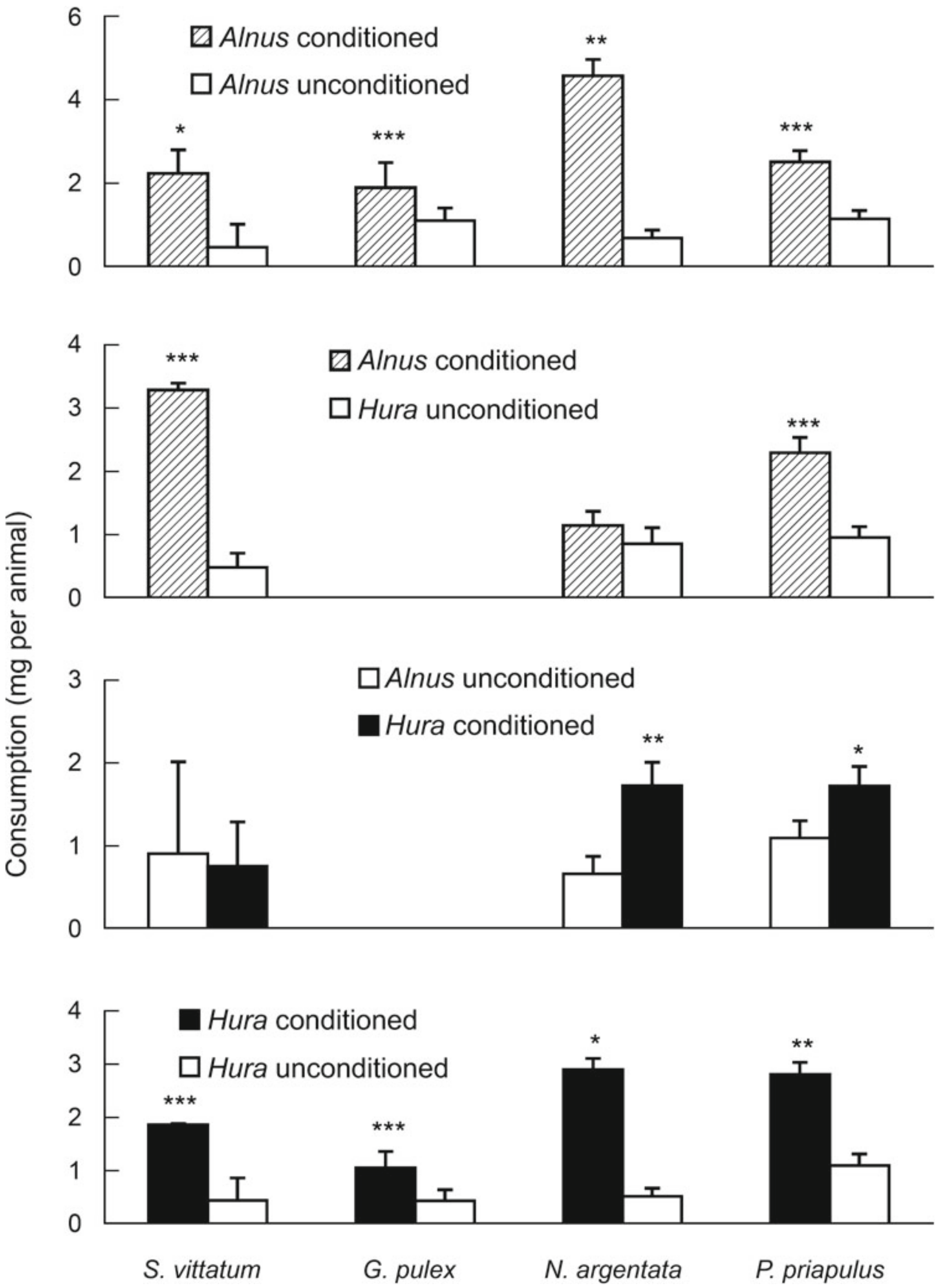

Fig. 9.2 Preference of tropical (*Nectopsyche argentata, Phylloicus priapulus*) and temperate (*Sericostoma vittatum, Gammarus pulex*) zone shredders for tropical (*Hura crepitans*) and temperate (*Alnus glutinosa*) conditioned and unconditioned leaves. Mean and one standard deviation are shown. (* = P < 0.05; **<0.01; ***<0.001) (Reproduced from Graca et al. 2001)

The importance of wood as a geomorphic agent in stream channels, altering flows and increasing habitat diversity, was discussed in Chap. 3. Wood can contribute 15–50% of total litter inputs in small, deciduous forest streams and even more in coniferous regions (Anderson and Sedell 1979). Wood is considered to be a minor energy resource because few invertebrates feed on it directly and wood appears to be a poor food. Although utilized only very slowly (a residence time of at least years to decades, in comparison to weeks to months for leaves), wood provides food and habitat for a number of species. Anderson et al. (1978) found some 40 taxa associated with this resource in wood-rich Oregon streams. Prominent aquatic xylophages included a midge (*Brilla*) which was an early colonizer of phloem on newly fallen branches, two species that gouged the microbially conditioned surface of waterlogged wood (the elmid, *Lara*, and the caddis, *Heteroplectron*), and a cranefly (*Lipsothrix*) that consumed nearly decomposed woody material. Invertebrate standing crop biomass on wood was about two orders of magnitude lower per kg of substrate than on leaf litter. The beetle *Lara avara* possesses robust mandibles capable of slicing away thin strips of wood, but apparently lacks digestive enzymes or gut symbionts to aid digestion. Microscopic inspection of material progressing through the gut indicated no change to the wood (Steedman and Anderson 1985); presumably the larva is nourished by microbiota and their exudates occurring on the wood surface. Not surprisingly, *L. avara* grows very slowly and requires 4–6 yrs to attain maturity. Wood fibers represented a high fraction (63%) of the gut contents of the caddis *Pycnocentria funerea* in streams draining a pine forest in New Zealand, and stable isotope analysis also indicated that most of its nourishment was derived from pine wood (Collier and Halliday 2000).

9.1.2 Consumers of FPOM

The collector:FPOM linkage (Fig. 9.3) depends on fine particulate organic matter captured from suspension or from substrates. Morphological and behavioral specializations for suspension feeding including setae, mouthbrushes, and fans are diverse and well studied (Wallace and Merritt 1980), whereas the mechanisms of deposit feeding appear to be less elaborate (Wotton 1994). FPOM originates in a number of ways. Categories considered to be richest in quality include sloughed periphyton and biofilm, and particles produced in the breakdown of CPOM. Collector-gatherers almost always are a major component of stream food webs and often are reported to be the dominant group present. In ten Hong Kong streams, FPOM was the major dietary component of macroinvertebrates in both shaded and unshaded streams, contributing over 50% of the diets of all primary consumers with the exception of obligate shredders and some scrapers (Li and Dudgeon 2008). Stable isotope signatures of FPOM was intermediate between CPOM and algae or cyanobacteria, indicating its mixed origin.

Caddis larvae in the superfamily Hydropsychoidea (comprised of the Philopotamidae, Psychomyiidae, Polycentropodidae, and Hydropsychidae) spin silken capture nets in a variety of elegant and intricate designs. Most net spinning caddis are passive filter feeders, constructing nets in exposed locations, but some nets act as snares (*Plectrocnemia*) or as depositional traps where undulations by the larvae create current (*Phylocentropus*) (Wallace and Malas 1976). Filter-feeding hydropsychids vary considerably in mesh size and microhabitat placement of their nets. There is evidence that catch nets of larger mesh tend to be found at higher velocities and capture larger prey, whereas fine mesh nets occur in microhabitats of low velocity and retain smaller particles (Wiggins and Mackay 1978). Members of the Arctopsychinae spin coarse nets, capture a good deal of animal prey and larger detritus, and tend to occur in headwaters. The Macronematinae occur in larger rivers, spin fine nets, and capture small particles. The Hydropsychinae are intermediate in net mesh size, more widely distributed, and perhaps because of the broad range of resources utilized, also are richer in genera.

Edler and Georgian (2004) examined the efficiency of particle capture in *Ceratopsyche morosa* (net mesh size

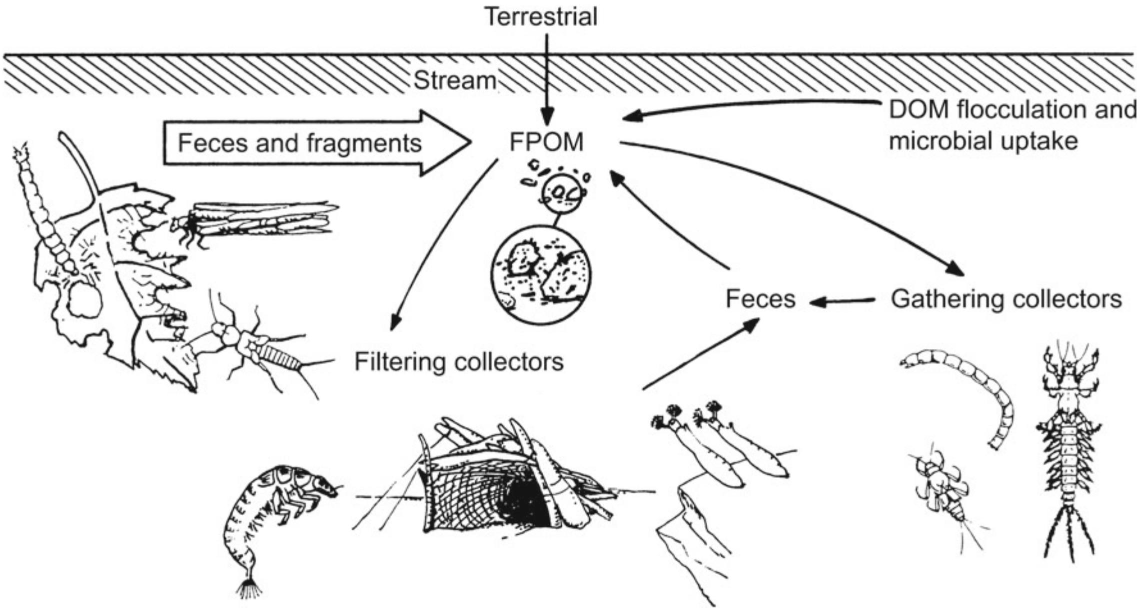

Fig. 9.3 The collector:FPOM linkages for a small stream within a temperate deciduous forest. Sources of detrital particles <1 mm include CPOM fragments, terrestrial inputs, animal feces, and sloughed algal cells and biofilm material. FPOM and associated microorganisms are ingested from the water column by filter feeders and from the streambed by collector-gatherers (Reproduced from Cummins and Klug 1979)

160 × 229 µm) and *C. sparna* (150 × 207 µm) by releasing food items of different sizes including *Artemia* nauplii (mean length 528 mm), and pollen of corn (*Zea mays*, mean diameter 84 mm) and paper mulberry (*Broussonetia papyrifera*, 12.5 mm). Both caddis species ingested more of the largest particles despite the greater availability of smaller particles in suspension (Fig. 9.4), but particles smaller than mesh openings are retained as well. Selective capture of larger particles might be expected to be energetically rewarding, and this is supported by the finding that *H. siltalai* nets retained a larger range of particles size (1–40 mm) than those observed in the water column (1–25 mm) (Brown et al. 2005). Because some captured particles were smaller than the mesh size of *H. siltalai's* net, adherence of particles to the silk apparently has some role in overall particle retention.

The impressive nets of caddis larvae are but one of the many specialized adaptations for capturing particles from suspension that have arisen repeatedly among aquatic invertebrates (Wallace and Merritt 1980). Larval black flies (Diptera: Simuliidae) are highly specialized suspension feeders (Fig. 9.5). Larvae attach to the substrate in rapid, often shallow water and extend their paired cephalic fans into the current (Currie and Craig 1988). Particles apparently are snared by sticky material on the primary fans, which are the main suspension-feeding organs, while secondary and medial fans act to slow and deflect the passage of particles. Food items are removed by the combing action of mandibular brushes and labral bristles, further adaptations to a filtering existence and lacking in some blackfly species that scrape substrates instead. Fans are opened when feeding and closed at other times (Crosskey 1990). The four species studied by Chance (1970) ingested particles from <1 µm to >350 µm. Field studies generally report the majority of ingested particles to be <10 µm in diameter (Merritt et al. 1982). Visualization of the fields of flow surrounding individual simuliid larvae indicates that they position their fans for maximum filtering effectiveness, and may be able to manipulate flow vortices to enhance feeding (Chance and Craig 1986; Lacoursiere and Craig 1993). Palmer and Craig (2000) suggest that black fly larvae occurring in fast-flowing, particle-rich water will tend to have strong fans with a porous ray structure, whereas larvae found in slow-flowing, particle-poor water will tend to have weak fans with a complex structure.

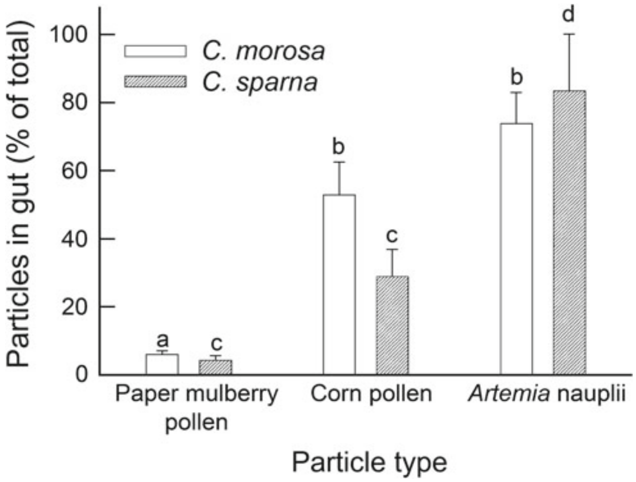

Fig. 9.4 Particles found in the guts of 5th-instar larvae of *Ceratopsyche morosa* and *C. sparna* as fractions of total. For each species, bars marked with the same letter are not significantly different (Reproduced from Edler and Georgian 2004)

Despite the evident elegance of the adaptations of larval simuliids for suspension feeding, this is by no means the only feeding mode employed. Currie and Craig (1988) state that scraping the substrate using mandibles and labrum is the second most important method of larval feeding, not including species that lack cephalic fans and are obligate scrapers. In addition, black fly larvae occasionally ingest animal prey, and Ciborowski et al. (1997) demonstrated that black fly larva grow when supplied only with dissolved organic matter. This diversity is a useful reminder that even those taxa displaying great specialization for a particular trophic role also may be capable of great versatility.

Larval black flies are important not only for their ability to filter very fine particles, but also for their production of fecal pellets. In northern rivers and particularly at lake outlets where very dense black fly aggregation occur, fecal pellet loads of several tons of carbon per day have been reported (Wotton and Malmqvist 2001). These pellets are available to filter feeders when in suspension, and to deposit feeders after they have sedimented. When Wotton et al. (1998) induced black fly larvae to produce labeled fecal pellets by adding paint to a lake-outlet stream, the guts of midge larvae, oligochaetes, and black fly larvae contained abundant label, and lesser amounts were found in baetid mayfly nymphs and the isopod *Asellus*.

Fecal pellets likely are an under-appreciated source of FPOM. Feces usually contain undigested food items and often are bound into discrete pellets, although some are diffuse (Wotton and Malmqvist 2001). Pellet size varies with the size of the animal that produced them, and can be as small as 6 × 9 µm in protozoans. Although most organisms produce fecal pellets that are smaller than the food they consume, some suspension feeders such as larval black flies can ingest very small food items and so produce fecal pellets larger than the food they ingest.

Other dipteran families with representatives adapted to a suspension-feeding existence in running waters include the Culicidae, Dixidae, and Chironomidae (Wallace and Merritt 1980). Some Chironominae construct tubes or burrows with catchments and create current by body undulations; others

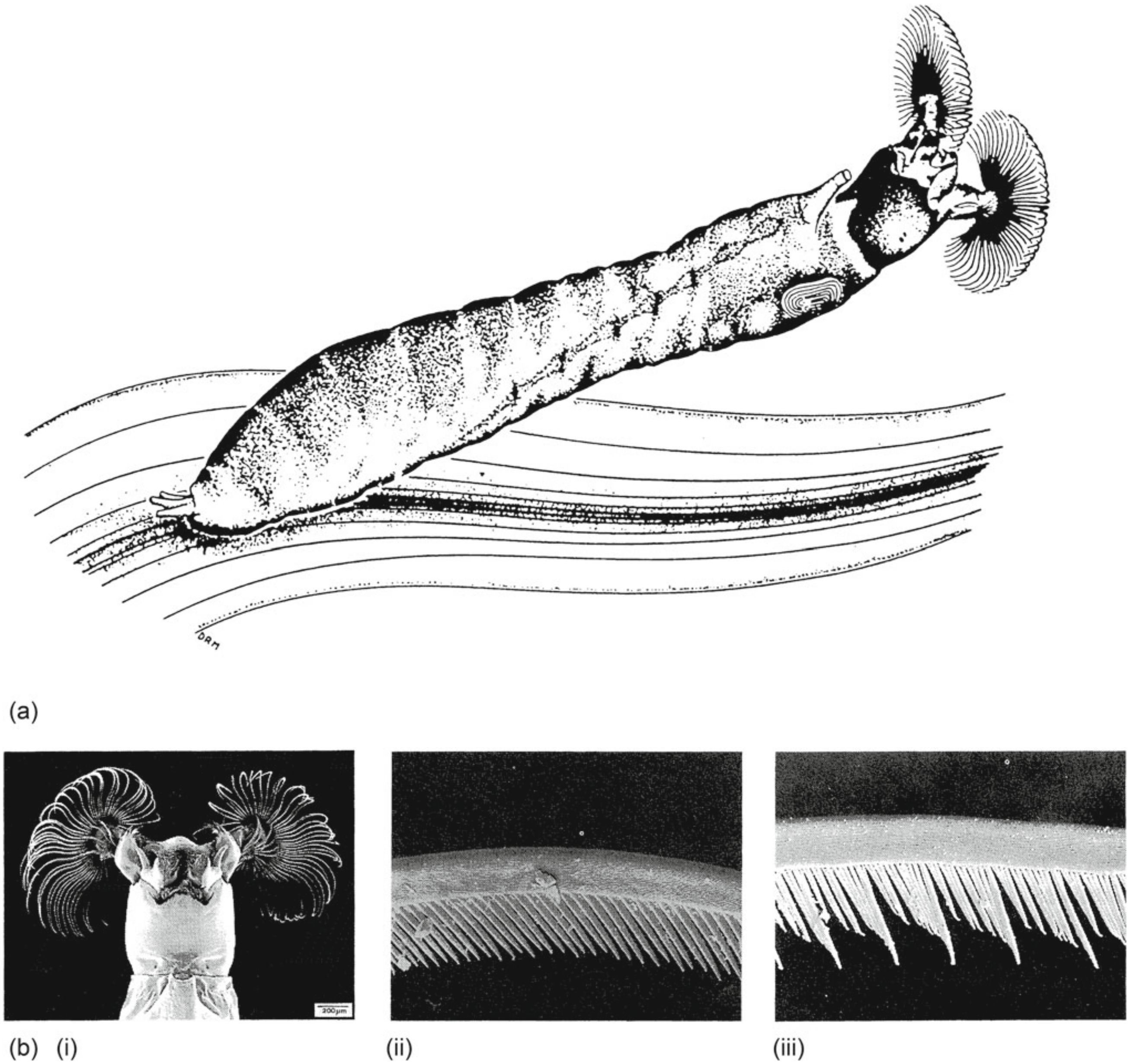

Fig. 9.5 (**a**) The typical filtering stance of a black fly larva (*Simulium vittatum* complex). The larval body extends downstream at progressively greater deflection from vertical with increasing current velocity, and is rotated 90–180º longitudinally as can be seen by following the line of the ventral nerve cord. The position of the paired cephalic fans is upper and lower, rather than side by side. The boundary layer (depth where $\bar{U}$ falls below 90% of mainstream flow) begins at roughly the height of the upper fan (Chance and Craig 1986). (**b**) Details of cephalic fans: left: head of a normal larvae seen from beneath, with cephalic fans fully open; middle: *Simulium atlanticum* with uniform fringe of microtrichia; right: *S. manense* with long and short microtrichia (Reproduced from Crosskey (1990) and SEM photographs of D.A. Craig)

such as *Rheotanytarsus* passively suspension-feed by means of a sticky secretion supported by rib-like structures on the anterior end of the case.

Bivalved mollusks are effective filter feeders, capable of removing very small particles (10 µm and smaller) from their respiratory water current using sieve-like modified gills and mucus to filter and trap particles. Bivalves can remove large amounts of FPOM from the water column, including detritus, bacterioplankton, phytoplankton, and zooplankton (Strayer 1999). Roditi et al. (1996) reported that zebra mussels removed phytoplankton and nonfood particles at the same rate, but other studies suggest that mussels can be selective within the FPOM pool. Based on stable isotope analyses, Nichols and Garling (2000) determined that unionids, which are the dominant group of freshwater mollusks, used bacteria as their main carbon source, although algae were found in the gut and provided vitamins and phytosterols. Christian et al. (2004) also found that mussels were using a bacterial fraction of FPOM as their food source based on stable isotope and digestive enzyme analyses. Although bivalves are traditionally seen as suspension feeders, Raikow et al. (2001) reported that stream unionids obtained 80% of their food from deposited material versus 20% from suspended material. These unionids were probably assimilating the microbial and algal components of the suspended or benthic organic matter rather the bulk material. Like black fly larvae, mussels can consume very small algae, and transform ingested particles into larger size organic matter through the production of feces and pseudofeces (Atkinson et al. 2011).

Mechanisms of FPOM feeding by collector-gatherers either are less diverse in comparison to suspension feeding, or less is known about the subject. Nonetheless, this feeding role is well-represented in most stream ecosystems in numbers of both individuals and species. Among the macroinvertebrates in swifter streams, representatives of the mayflies, caddisflies, midges, crustaceans, and gastropod mollusks are prominent deposit feeders consuming small particles from the benthos. In slow currents and fine sediments one would also expect to find oligochaetes, nematodes, and other members of the meiofauna. It would be surprising if these animals all fed in the same way and consumed the same food. In addition to their particular food-gathering morphologies, these taxa differ in their ability to produce mucus, in mobility and body size, in their digestive capabilities, and in whether they are surface-dwellers or live within the sediments.

Browsing on easily assimilated biofilms may allow consumers to meet their energy needs without having to ingest large quantities of material. This is not the case for animals that ingest low-quality POM mixed with sediments. Many deposit feeders "bulk-feed", processing each day from one to many times their body mass of sediments and assimilating a low fraction of what they ingest. The burrowing mayfly *Hexagenia limbata* ingests more than 100% of its dry mass daily (Zimmerman and Wissing 1978). The assimilation efficiency of FPOM collectors in Sycamore Creek, Arizona, was estimated at 7–15%, and they consumed the equivalent of their body weight every 4–6 h (Fisher and Gray 1983). High quality foods that can be absorbed rapidly should favor high feeding rates and short retention times, whereas feeding should slow to allow longer digestion of poor quality foods. Calow (1975a) demonstrated an inverse relation between ingestion rate and absorption efficiency in two freshwater gastropods. When starved, snails slowed the rate of passage of food through the hepatopancreas, the main site of absorption and digestion. The effect of changing food quality on gut retention time apparently varies with the quality of the food, however. Calow (1975b) found that the herbivorous limpet *Ancylus fluviatilis* increased its retention time for poor quality food (the expected result), but the detritivorous snail *Planorbis contortus* did the opposite. It may be that whenever the food carrier is highly recalcitrant, as in the case of lignin, it pays to process material rapidly for easily removed microbes rather than attempt to extract energy from nearly indigestible substrate.

9.1.3 Herbivory

The *grazer:periphyton* and *piercer:macrophyte* linkages (Fig. 9.6) are the principal pathways for the ingestion of living primary producers by invertebrates. The latter refers primarily to the microcaddisflies (Hydroptilidae), which pierce individual cells of algal filaments and imbibe cell fluids (Cummins and Klug 1979). Descriptions of the grazing pathway typically focus on attributes of the periphyton mat and the mode of invertebrate herbivory. The periphyton, comprised mainly of diatoms, green algae, and cyanobacteria, are found almost everywhere in running waters (Chap. 6). The extent of herbivory varies with algal growth form and differs among the major taxonomic groups for reasons discussed further in Chap. 10, but it appears that virtually all benthic algae serve as food for some grazing animal.

Morphological specialization of grazing invertebrates includes the blade–like mandibles of glossosomatid caddis larvae, the rasping radula of snails, chewing mouthparts of some mayflies and brush–like structures of others, piercing mandibles of hydroptilid caddis larvae, and so on. These are described as scrapers, grazers, and piercers, respectively. Other FFGs likely ingest plant matter occasionally. Collector–gatherers surely consume loose algae along with microbes and detritus (Lamberti and Moore 1984), and shredders benefit from the presence of an attached flora growing on the surface of fallen leaves, as mentioned earlier. Drifting diatoms and algae also are captured by suspension feeders, especially those taxa possessing fine sieving devices (philopotomid caddisflies, some chironomid and black fly larvae), and even the relatively coarse meshes of most hydropsychids retain some diatom and algal cells. Indeed, within the North American insect fauna, consumption of algae has been noted in at least six orders and 38 families (Merritt et al. 2019). Moreover, the composition of an herbivore's diet changes with many factors, including age, season, food availability, and location.

Just as animals differ in their mode of feeding, members of the periphyton differ in a number of ways that affect their overall vulnerability to particular herbivores. Benthic algae vary markedly in growth form and mode of attachment as well as in overall size (Fig. 6.1), and this must affect their availability to particular kinds of grazers. For example, field

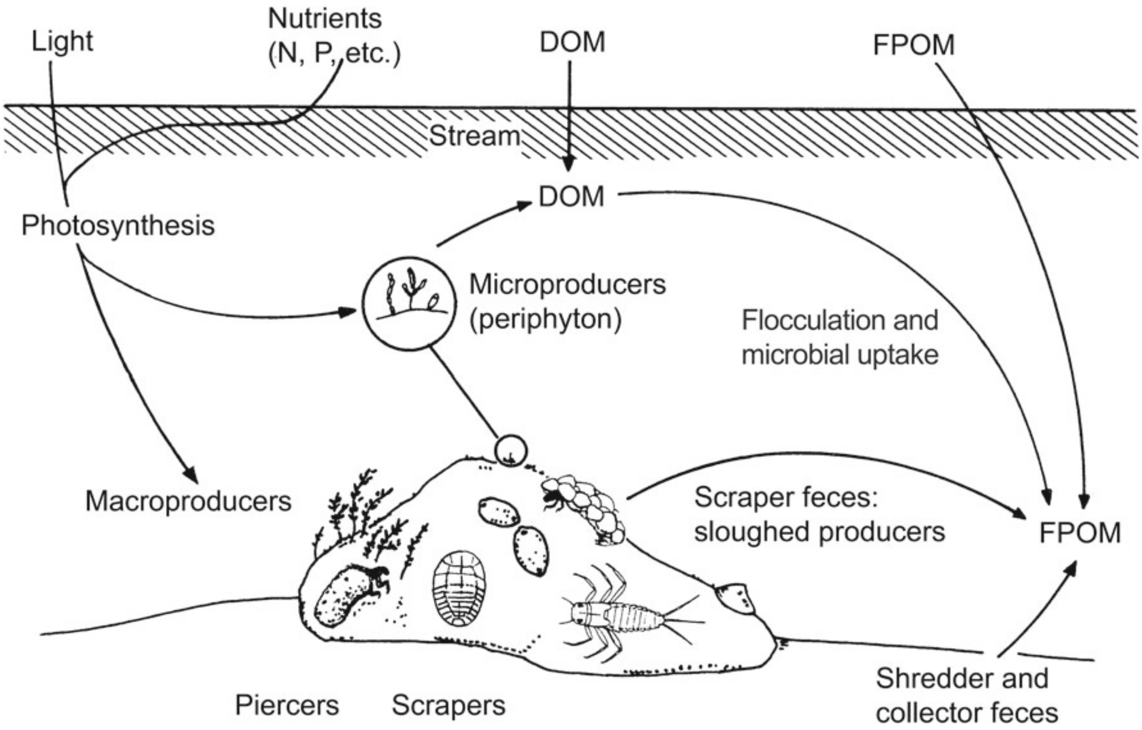

Fig. 9.6 The grazer:periphyton and piercer:macrophyte linkages for a temperate stream. The periphyton-biofilm organic layer on substrate surfaces is scraped or browsed depending on the consumer's mode of feeding. Diatoms and other algae are important constituent of this basal resource, but consumers also may ingest detritus, microorganisms, and occasional very small invertebrates. Piercers such as caddis larvae (Hydroptilidae) imbibe cell fluids through the cell walls of macroalgae (Reproduced from Cummins and Klug 1979)

manipulations of grazer densities in a California stream established that the mayfly *Ameletus* with collector-gatherer mouthparts was most effective with loosely attached diatoms. In contrast, the stout, heavily sclerotized mandibles of the caddis *Neophylax* were effective against tightly adherent diatoms (Hill and Knight 1988). Filamentous algae apparently are difficult for grazing insects to harvest or digest, and so they are consumed principally as new growths (Lamberti and Resh 1983). To the snail *Lymnaea*, however, possessing both a radula for their harvest and a gizzard for their mechanical breakdown, filamentous green algae provide a very satisfactory diet.

The assimilation efficiencies of herbivore-detritivores fed different diets are a useful measure of the wide range of nutritional value of various foods. Based on a review of 45 published values for 20 species of aquatic insects, assimilation efficiencies range from 70–95% on a diet of animal prey, 30–60% for a variety of algal and periphyton diets, and from 5–30% on a diet of detritus (Pandian and Peter 1986). Considerable variation can occur even for a single species feeding on periphyton. Assimilation efficiencies for the snail *Juga silicula* were as high as 70–80% when first added to laboratory streams, but values declined during the course of the study to as low as 40% (Lamberti et al. 1987). This coincided with a shift in composition of the periphyton from diatoms and unicellular green algae to filamentous green algae and cyanobacteria. The decline in assimilation efficiency could be the result of cell senescence and other changes in physiological condition, or a decline in nutritional value owing to successional changes in the periphyton assemblage.

The wide range of assimilation efficiencies observed with periphyton diets is at least partly due to their structural and biochemical characteristics. Variation in protein and lipid content and in cell wall thickness likely is responsible for differences among autotrophs in their nutritional value and palatability. Too high a ratio of carbon to nitrogen makes for a poor diet, indicating a high cellulose and lignin content and a low protein content; in general C:N ratios should be less than 17:1 for animal utilization. On this basis, members of the periphyton appear to be generally suitable (C:N ranges from 4-8:1), whereas aquatic vascular macrophytes appear to be nutritionally less adequate (C:N from 13-69:1) (Gregory 1983). Variation in the nitrogen content of diets was an extremely effective predictor of assimilation efficiency for twenty taxa of aquatic insects reviewed by Pandian and Peter (1986).

Lipid content is another variable likely to influence the nutrition and development of herbivores. Most insects are unable to synthesize polyunsaturated fatty acids and sterols, indicating that the lipid content of their diets is important to food quality. Intense grazing by a snail and a larval caddisfly in laboratory streams altered the fatty acid composition of the periphyton, suggesting that grazing may have been responsive to this aspect of diet quality (Steinman et al. 1987). Cargill et al. (1985) showed that specific fatty acids were critical dietary components to a detritivorous caddis larva, *Clistoronia magnifica*. More generally, the higher algal polyunsaturated fatty-acid (PUFA) content of stream algae is a principal reason why algae are a higher quality food source than dead leaves or even microbes (Guo et al. 2016).

Cyanobacteria are considered to be a poor food supply for freshwater plankton feeders (Wetzel 2001) and possibly for periphyton grazers as well. Cyanobacteria may have a high protein content, but other attributes, including a polymucosaccharide sheath rendering cell walls resistant to digestion, perhaps toxins, and a filamentous growth form all detract from their value as food. However, the evidence from lotic grazers is mixed. For example, in laboratory feeding trials the mayfly *Tricorythodes minutus* ate and assimilated two cyanobacteria, *Anabaena* and *Lyngbya* (McCullough et al. 1979), whereas *Asellus* and *Gammarus* would not consume *Phormidium* (Moore 1975). The nutritional inadequacy of cyanobacteria for gammarids and potentially other benthic invertebrates appears to be at least partially due to a deficiency in certain lipids, as a cyanobacterial diet supplemented with certain lipids markedly improved gammarid growth and survival (Gergs et al. 2014).

Macrophytes of rivers and streams traditionally have been thought to enter food webs primarily as detritus, as their tough cell walls and high lignin content that provide structural support are barriers to herbivore consumption of living plants. More recent syntheses of a large number of experimental studies across all types of freshwater ecosystems suggest this view is incorrect, and indicate that herbivores can remove up to half of all macrophyte biomass as living tissue (Bakker et al. 2016; Wood et al. 2017). Submerged macrophytes require less support tissue than emergent forms, and experience higher rates of herbivory, as one would expect. Herbivorous taxa include some aquatic insects, crayfish, and snails among the invertebrates; some fishes including Asian carps, and a number of leaf, fruit, and seed eating fishes of the tropics; ducks and other waterfowl; and semi-aquatic mammals such as the muskrat of North America and capybara of South America (discussed further in Sect. 9.3). Macrophytes typically are most abundant in large rivers with associated floodplains, lakes, and backwaters, and these habitats are likely to also support the greatest abundance of their consumers.

Intriguingly, the most dramatic effects of invertebrate grazing on living aquatic macrophytes involve herbivores derived mainly from terrestrial insect lineages. These include chrysomelid and curculionid beetles, aquatic and semi-aquatic lepidopterans, and specialized dipterans (Newman 1991). At a site in the Ogeechee River, Georgia, infested with the waterlily leaf beetle *Pyrrhalta nymphacaeae* (Chrysomelidae), leaves of the waterlily *Nuphar luteum* lasted only 17 days compared to more than 6 weeks at another site where the beetle was absent (Wallace and O'Hop 1985). In Brazilian rivers, the native apple snail (*Pomacea canaliculata*) significantly reduced biomass accrual of *Hydrilla verticillate*, a submerged, rooted macrophyte native to Asia and Australia, but did not appear capable of fully suppressing its establishment (Calvo et al. 2019). Some free-floating macrophytes, including the water hyacinth *Eichhornia crassipes* and the giant salvinia, *Salvinia molesta*, can become so abundant that they present serious weed-control problems worldwide, particularly in the sub-tropics and tropics. The salvinia weevil (*Cyrtobagous salviniae*, Curculionidae), a natural enemy of giant salvinia in South America, has been introduced around the world as a biological control agent, and in most instances has reduced plant abundance to acceptable levels. Giant salvinia occurs in at least at least 12 states in the southern US, and where weevils have been released, plant coverage has been dramatically reduced (Tipping et al. 2008).

9.1.4 Predaceous Invertebrates

The *predator:prey linkage* (Fig. 9.7) is ubiquitous. All animals are prey at some stage of their life cycle, and predaceous invertebrates occur in all sizes, from protozoans that engulf other protozoans, to insects and crustaceans capable of ingesting large invertebrates and small fish. Most predators engulf their prey entire or in pieces, but snipe flies (Diptera: Athericidae) and some hemipterans have piercing mouthparts (Cummins 1973). Other distinctions can be made between hunting by ambush versus searching (Peckarsky 1984), and whether prey are obtained from suspension, as in some hydropsychids, or strictly from the substratum, as in flatworms. Occasional predation probably is widespread, particularly the ingestion of micrometazoans, protozoans, and early life history stages of macroinvertebrates. Such unpremeditated carnivory may provide high quality protein needed by many invertebrates to complete their life cycles, and also may form an important link between microbial and macro-consumer food webs.

Mechanical detection is a widespread and varied modality for sensing prey. In many instances this means actual contact, for instance with antennae and setal fringes of limbs as in the stonefly *Dinocras cephalotes* (Sjostrom 1985). Vibrations in the water or of capture nets also serve as signals, as in the hemipteran *Notonecta* (Lang 1980), which captures prey on the water surface, and net-spinning caddis

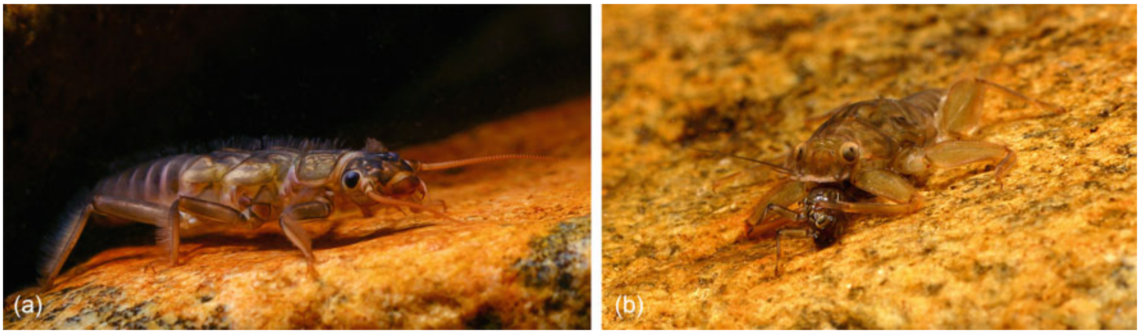

Fig. 9.7 Two predaceous invertebrates common in streams of the Rocky Mountains, US. (**a**) The stonefly *Megarcys signata*, (**b**) the mayfly *Drunella* devouring *Baetis*, also a mayfly. Photos courtesy of Angus McIntosh

larvae that detect vibrations of prey in their nets (Tachet 1977). Visual cues likely are less important to invertebrate predators, because eyes are not well developed and many species dwell in crevices or are not active by day, but odonates, some heteropterans, and gyrinid beetles rely more on vision (Peckarsky 1984). Larval *Libellula depressa* (Odonata) were observed to strike at a mayfly nymph in response to either mechanical or visual cues, but mechanical cues were primary and did not require contact, and chemical cues apparently were ineffective (Rebora et al. 2004). Indeed, chemical detection of prey is important only in a few predaceous insects in the Hydrometridae and Dytiscidae, but it may be important in other invertebrates. Lake-dwelling triclads exhibit a chemosensory response to their isopod prey (Bellamy and Reynoldson 1974), and presumably stream-dwelling triclads do so also. The water mite *Unionicola crassipes* locates prey primarily by mechanoreception and vision, but it also becomes more sedentary in prey-conditioned water, suggesting that chemical detection promotes area-restricted search behaviors that presumably enhance encounter rates (Proctor and Pritchard 1990).

Sit-and-wait predators include those that simply remain motionless until the prey approaches within striking range, and those that trap their prey using nets (e.g., caddis larvae) or mucus trails (e.g., flatworms). Odonates that usually ambush also will stalk prey, a behavior that may be influenced by hunger level or their own risk of predation. Sjostrom (1985) reported that *D. cephalotes* searched in darkness, but was primarily a sit-and-wait predator in very low light. Risk from its own predators is the most likely explanation, although ability of prey to escape may be an additional factor. Predators often are undiscriminating in their diets, capturing whatever they encounter that is small enough to subdue. Aspects of the predator that bias it towards consuming more of some prey than others include sensory capabilities, foraging mode, and behavioral mechanism of prey capture. For prey, many aspects of body plan, life style, and behavior influence their vulnerability. These traits of predator and prey are not easily separated. From the many studies of the diet of predaceous invertebrates, usually based on gut analyses and behavioral observations, body size, prey availability, and prey vulnerability are of particular importance in determining what is eaten.

Size relationships between predators and their prey as well as within a guild of invertebrate predators are of critical importance to food web relationships, a topic discussed in greater detail in Sect. 10.2. Typically, the average size of ingested prey increases with size of predator, as does the variety of prey items consumed. Predaceous stoneflies tend to ingest diatoms and other non-animal items when very small. Diet changes gradually over development, often consisting primarily of chironomids in early instars, and then broadening to include a menu in which mayflies, simuliids, and trichopterans supplement and may eventually replace midge larvae as prey. Although some differences are reported among species and study locales, presumably reflecting differing availability of prey, any two stoneflies of about the same size, when in similar habitats, consume diets of similar species composition. By measuring head widths of ingested prey and converting those values to dry mass, Allan (1982) showed a very similar positive relationship between prey size and predator size for several species of predaceous stoneflies and the two most common prey, *Baetis* and Chironomidae (Fig. 9.8). With an increase in the size of prey ingested there usually is an increase in diet breadth as well. Small predators tend to have less diverse diets because they don't reach sufficient size to capture prey larger and more agile than midge larvae.

Analysis of gut contents typically reveals a good correlation between what is eaten and what is available. The rank order of prey taxa in the diet of large *Hesperoperla pacifica* was similar to the rank order of prey in the benthos (Allan and Flecker 1988). There is some evidence that prey availability is such a decisive factor that it may override differences between predators in foraging mode. The net-spinning *P. conspersa* and the more mobile *S. fuliginosa* exhibited considerable overlap in habitat use and diet, although the former consumed more terrestrial items, large stoneflies, and

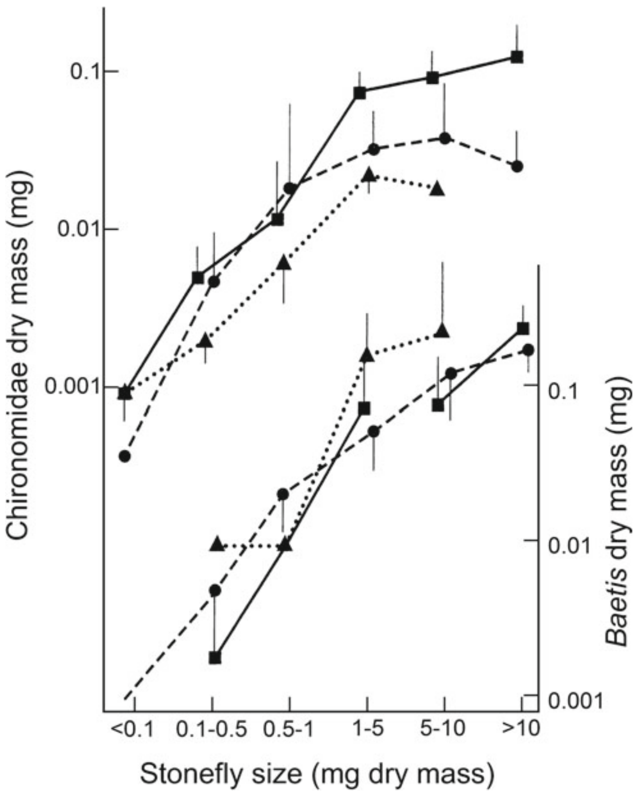

Fig. 9.8 Average dry mass of prey found in the foreguts of three species of predaceous stoneflies, as a function of size groupings of predators. Stoneflies of a particular size consumed prey of the same size for both prey species. Means and 95% confidence limits are shown for *Megarcys signata* (■), *Kogotus modestus* (▲), and *Hesperoperla pacifica* (●) (Reproduced from Allan 1982)

small chironomids, which apparently were more easily trapped in the net of *P. conspersa* (Strategies et al. 1979).

9.1.5 Patterns in FFG Composition

A number of studies have examined the correspondence between FFG composition and basal resources, often within the framework of the River Continuum Concept (Fig. 1.1), which describes changes in basal resources with stream size and order. Terrestrial leaf litter should dominate in shaded headwaters, benthic algae should be most abundant in the wide but relatively shallow mid-order river sections, and FPOM derived from upstream and floodplain sources should be most important in deeper and more turbid lower river sections. The composition of FFG is expected to mirror these changes. In addition, FFGs should respond to differences in terrestrial vegetation: headwaters in open meadows should support more benthic algae and more scrapers, as should stream sections where forest harvest has opened the canopy.

A survey of invertebrate FFGs in streams ranging from first to seventh order in the Cascade Range of Oregon, US, found reasonable correspondence with the river continuum model (Hawkins and Sedell 1981). Shredders dominated upper, shaded reaches, scrapers were most important in intermediate-sized sections, collectors increased in importance downstream, and predators were nearly constant in relative abundance at all sections. In addition, shredder numerical abundance was significantly correlated with CPOM biomass, scraper abundance correlated with chlorophyll *a* on cobbles, and the abundance of invertebrate predators correlated with the abundance of invertebrate prey. Sampling eleven sites along the river continuum of the Little Tennessee River, North Carolina, US, from a first-order headwater stream to a seventh-order site, classifying taxa into FFGs, and estimating proportional representation using biomass, Grubaugh et al. (1996) found FFG abundance was strongly related to habitat diversity. Collector-filterers generally dominated in cobble and bedrock areas, collector-gatherers in pebble-gravel, and shredders and collector-gatherers in depositional habitats. After weighting FFG biomass according to relative habitat availability among sites, benthic community composition was consistent with predictions of the river continuum concept (Fig. 9.9). In a subsequent study conducted at 5th through 7th-order sites in the same system, employing detailed gut content analyses, leaf detritus consumption decreased with increasing stream order, and consumption of amorphous fine particles increased (Rosi-Marshall and Wallace 2002), again broadly consistent with expectations outlined by the river continuum model. Similarly, FFG distribution showed partial agreement with expected longitudinal changes from headwaters to mid-order in a Puerto Rican stream (Greathouse and Pringle 2006). Shredders decreased, scrapers increased, and predators remained unchanged, as expected. The downstream decrease in filterers normally would be unexpected, but in this system may be explained by the high abundance of filtering atyid shrimp in the headwaters.

In contrast, a number of studies have found poor or no correspondence between FFGs and expectations of trophic diversity based on riparian forest cover. In a comparison of open and closed canopy streams in the western Cascade Mountains of Oregon, US, Hawkins et al. (1982) found that open streams had higher abundances of invertebrates, including of collector-gatherer, filter feeder, herbivore shredder and piercer, and predator FFGs. Moreover, neither shredders nor scrapers exhibited a marked difference in density among canopy types. The distribution of feeding groups along the LaTrobe River, Victoria, Australia, showed some similarity with predictions of the river continuum concept, although habitat played a role (scrapers were most abundant at cobble sites, and filterers avoided sand), and shredders did not decrease downstream as expected (Marchant et al. 1985).

There is much evidence that the presence and importance of shredders vary regionally, being generally scarcer in

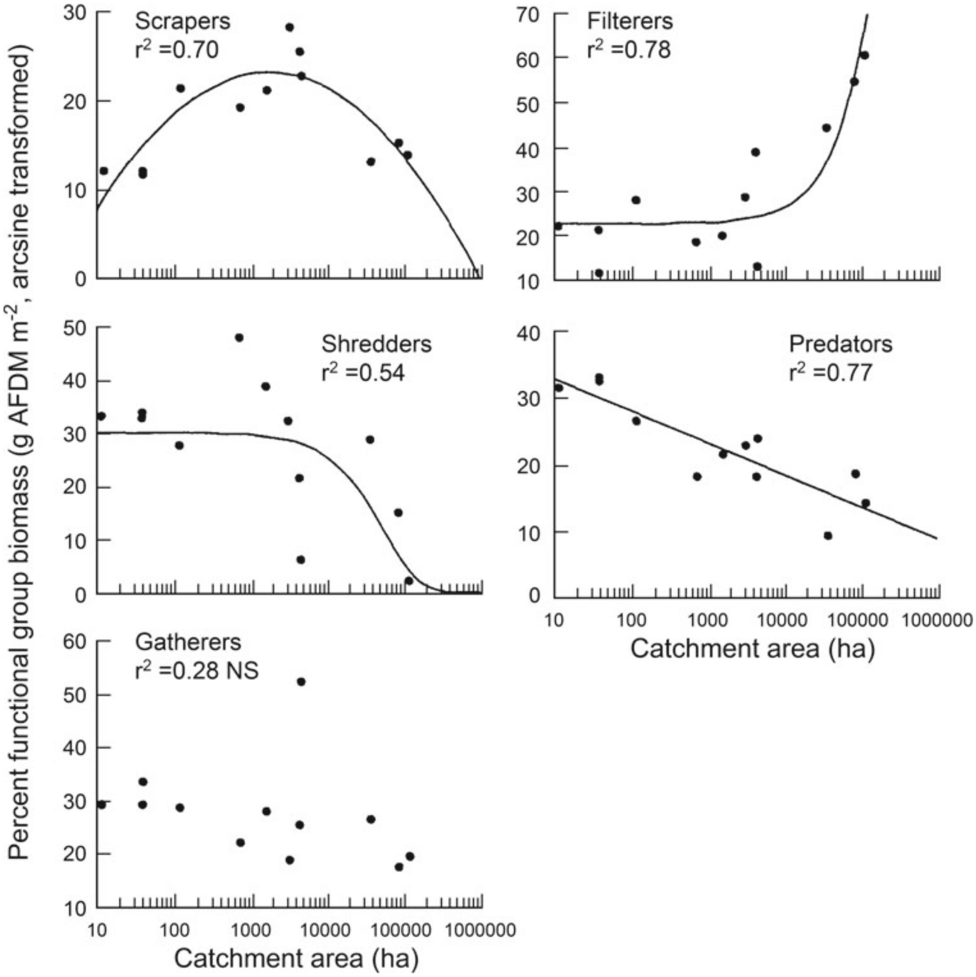

Fig. 9.9 Relationships between relative dominance of feeding groups and catchment area in the Ball Creek—Coweeta Creek—Little Tennessee River continuum. Dominance is expressed as percentages of total habitat-weighted biomass at each sampling station (Reproduced from Grubaugh et al. 1996)

tropical systems. Important shredders of the Northern Hemisphere, including the caddisfly family Limnephilidae, certain plecopteran stoneflies, and certain crustaceans (amphipods and isopods), are weakly represented in the Neotropics. A global analysis of 129 stream sites from 14 regions on six continents did indeed show shredders to be more abundant and diverse in temperate than in tropical streams, with an inverse correlation with temperature, but no relationship with leaf toughness, a measure of leaf palatability (Boyero et al. 2011). The number of shredder taxa was found to be low in some tropical regions (Central America and the Caribbean) but not in others in South America, Asia, and Australia, indicating that shredder distribution is related to biogeography as well as to latitude.

Scarcity of shredding insects implies that microbes are the primary agents of leaf breakdown in those locations. Fresh leaves of several tree species underwent rapid decomposition in a tropical stream in in Mato Grosso, Brazil, but no shredder activity was observed, indicating that biological breakdown was primarily microbial (Wantzen and Wagner 2006). Where they occur, it may be that tropical shredders must be flexible in their diet, due to a less predictable supply of leaf litter. A gut content analysis of *Phylloicus* larvae (Trichoptera: Calamoceratidae) in sites in southeastern Brazil with differing amounts of riparian vegetation demonstrated that this insect, which is commonly classified as a shredder, had greater amounts of CPOM in their guts at sites with riparian vegetation, but contents were dominated by FPOM at sites without extensive riparian habitat (Ferreira et al. 2015). It should also be noted that while insect shredders of terrestrial leaf litter often are rare in tropical streams, decapod shrimp and crabs, large omnivores able to tear apart tough leaves, can be abundant.

Several explanations have been proposed for the scarcity of shredders in the tropics. Chief among these are the ideas that shredders are from lineages that evolved in cool waters, and so are physiologically poorly adapted to the warmer waters of the tropics (Dobson et al. 2002); and that leaves in tropical streams are both scarce and less palatable, due to better defenses against herbivory (Wantzen et al. 2002), greater toughness, and reduced nutrient concentrations. Indeed, a comparison of leaves of three tropical tree species from French Guyana with leaves of four tree species from Germany found litter quality of tropical leaves to be clearly lower than that of three of the four temperate species, as evidenced by phosphorus content and leaf toughness (Bruder et al. 2014). Similarly, leaves from Venezuela were found to be of greater toughness than leaves from Portugal, and species of shredder preferentially consumed softer leaves (Graça and Cressa 2010). In addition, tropical macroinvertebrates tend to be smaller in body size than temperate zone taxa, and small size may limit ability to break up large pieces of CPOM. The presence of a diverse and specialized shredder FFG in north temperate streams likely is favored by predictable leaf fall during autumn, more synchronized leaf abscission, potentially less mechanical or chemical protection against herbivory, and, relative to the tropics, fewer species of trees (Wantzen and Wagner 2006).

Anthropogenic change can shift FFG relative composition, often (but not always) seen in response to altered land use. Urban streams typically have fewer individuals and less taxonomic diversity than rural counterparts (Walsh et al. 2005; Booth et al. 2016). Depending on the type and intensity of urban stressors, invertebrate functional group representation may also be affected. Taxon richness, diversity metrics, and pollution-intolerant EPT taxa all declined with increasing urbanization across 43 streams in southeastern Wisconsin, US (Stepenuck et al. 2002). Proportional representation of collectors and gatherers increased along the urbanization gradient, while proportions of filterers, scrapers, and shredders decreased with increased watershed imperviousness (Fig. 9.10). Urban streams in northern Maryland, US, experienced a 50% loss of predator taxa and up to 70% loss of collector taxa relative to streams in agricultural settings (Moore and Palmer 2005). Aquatic insect species were fewer and smaller at downstream urban compared with upstream rural sites in five streams in New York, US (Lundquist and Zhu 2018). Urban sites supported significantly less biomass of shredders and predators; collector-gatherers were the most abundant and diverse group overall, and were not markedly less diverse at the urban sites. Studies frequently find a significant increase in the proportion of collector–gatherers with urbanization (Stepenuck et al. 2002; Compin and Cereghino 2007; Sterling et al. 2016), and a decline in predator representation is also common (Smith and Lamp 2008; Sterling et al. 2016). Using percent imperviousness to compare urban, suburban, mixed-use, and rural watersheds in the upper Oconee River basin, Georgia, US, Sterling et al. (2016) observed a decline in biomass of predators, scrapers, and shredders with increasing impervious cover, while dominance by collector-gatherers increased. Oligochaetes and non-predatory chironomids comprised 60–90% of macroinvertebrate biomass at highly urbanized sites.

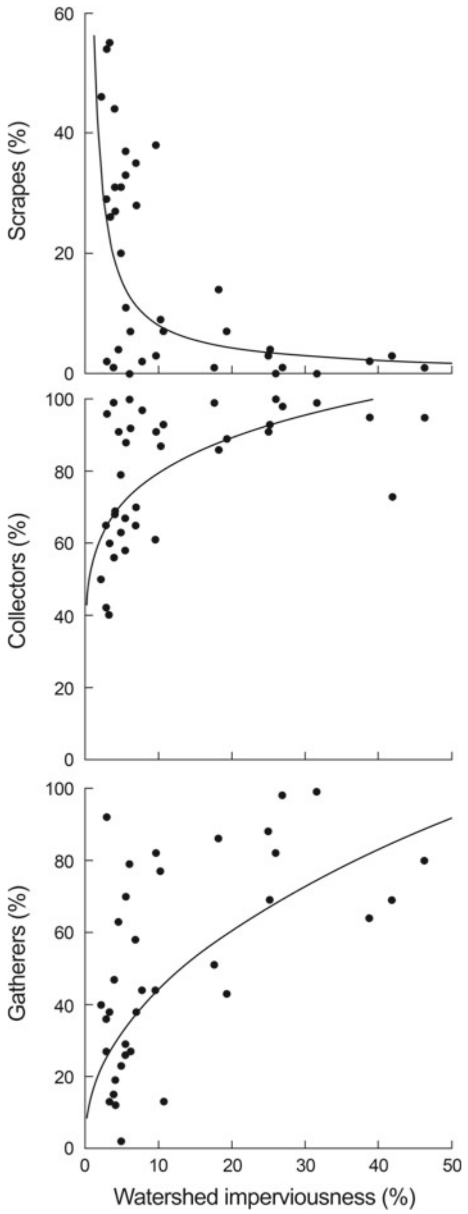

Fig. 9.10 The relative abundance of scrapers, collectors, and gatherers in relation to percent watershed imperviousness at riffle habitats in 43 streams from southeastern Wisconsin, US (Reproduced from Stepenuck et al. 2002)

9.1.6 Assimilation-Based Analyses of Feeding Roles

Traditional methods for investigating the feeding roles of invertebrate species include gut-content analysis, fecal analysis, and behavioral observations. Such information can provide important confirmation of FFG classification, as well as examples of flexible and opportunistic feeding that call into question the utility of FFG classification. Examples exist of algal consumption by predatory (Lancaster et al.

2005) and leaf-shredding (Dangles 2002) invertebrates. Within the scraper category, some *Glossosoma* caddis larvae were found to feed selectively on the algal components of biofilms while heptageniid mayflies consumed bulk biofilm (McNeely et al. 2006). Typically classified as a shredder feeding on leaf litter and associated microbes, the many species of *Gammarus* are actually able to exploit a far wider food base as a facultative herbivore and predator (MacNeil et al. 1997). Comparing the FFG assignment for fifty-six benthic macroinvertebrates where growth or isotope studies provided additional information about resource use, Mihuc (1997) found that half or more of gatherers, scrapers, and shredders consumed resources not indicated by FFG identity, suggesting that they should be classified as generalists. If flexible feeding is indeed widespread, then FFG classification may have limited success in identifying the relative importance of different basal resources, and the extent to which stream energy pathways are predominantly allochthonous or autochthonous.

Recent years have seen broader use of powerful new tools that provide fresh insight into the energy sources that consumers assimilate into their tissue (Post 2002; Finlay et al. 2010). As described earlier, stable isotopes of C, N, and H are becoming widely used as food web tracers in aquatic ecosystems, providing evidence on trophic position and the relative importance of autochthonous versus allochthonous basal resources. Fatty acid analysis can also reveal the importance of algae to a consumer's assimilation and growth, and even in apex predators can reveal the food web pathway of primary importance.

From assimilation-based analyses, a number of studies have found that algae are more important as a basal resource than might traditionally have been expected. In tropical Hong Kong streams, isotope and fatty acid analysis showed that algal sources contributed more than terrestrial sources to the biomass of a snail and two species of shrimp, despite the predominance of terrestrial detritus inputs (Lau et al. 2009). Fine particulates were a more important energy source than leaf litter in most comparisons, attributed to the former's lower C:N ratio and higher palatability. In the Eel River, California, where previous studies have found shredders to consume both terrestrial detritus and algae, shredders spanned a range of $\delta^{13}C$ and δD values from those consistent with consumption of terrestrial detritus to values enriched in ^{13}C and depleted in ^{2}H, indicating near-complete reliance on algae growing in pool habitats where algal $\delta^{13}C$ was highly enriched (Finlay et al. 2010).

Evidence that the contribution of algal resources to lotic food webs often has been underestimated, especially in shaded streams receiving abundant leaf fall, is one of the most consistent and intriguing outcomes of stable isotope analyses. Using $\delta^{2}H$ enrichment as a measure of consumer reliance on allochthonous resources, Collins et al. (2016) found considerable flexibility in macroinvertebrate feeding across a range of stream conditions in New York, US, and on the island of Trinidad. Their results were not greatly inconsistent with FFG expectations: scrapers showed the highest reliance on autochthonous energy, predators and shredders made the most use of allochthonous resources, and collector gatherers and filterers spanned a broad range of energy use. However, even shredders relied partly on autochthonous energy, depending on the resource base available for consumption, and grazers consumed mostly allochthonous material in some circumstances. Strong reliance on allochthony by predators presumably reflected the food resources of their prey, and for fishes likely indicated their reliance on terrestrial invertebrates that fell into the stream. Flexibility in feeding, as seen in degree of reliance on allochthonous energy, was significantly related to canopy cover for most taxonomic groups (Fig. 9.11). In the tropical streams of Trinidad, reliance on autochthonous energy sources was even more pronounced, and even more strongly related to a gradient in canopy cover.

Interestingly, the argument that autochthony may be under-estimated has been advocated both recently (Vadeboncoeur and Power 2017) and much earlier. In a counterpoint to the then-widely accepted paradigm that allochthonous energy primarily in the form of leaf fall was the main energy source for streams, Minshall (1978) argued that autotrophic production often is the major or sole source of fixed carbon supplied to stream ecosystems, and can be important in streams considered to be primarily heterotrophic. His compilation of then-available data for a number of streams indicated that heavily forested headwater streams did tend to derive most of their fixed carbon from outside the system, whereas high values for instream production were associated with grassland and desert regions, and the larger, more open forest streams of the deciduous and semi-arid Rocky Mountain areas. As more evidence from assimilation-based studies accumulates, it is apparent that benthic algae can be an important basal resource even in settings where their role has previously been thought to be modest.

In closing, it is worth noting that despite the limitations of FFG classification, this approach remains in wide use. FFG tables in Merritt et al. (2019) recognize the challenge of accurately classifying taxa into feeding groups by providing both primary and secondary designations, and mention of facultative feeding where known, thereby helping to distinguish obligate (specialist) from facultative (generalist) taxa. The ease with which an investigator can translate information on the relative abundance of taxa at a site into a depiction of likely energy pathways within the food web makes this approach extremely useful. Shifts in the proportional representation of FFGs along, for example, an urban gradient, can reveal how anthropogenic change likely is

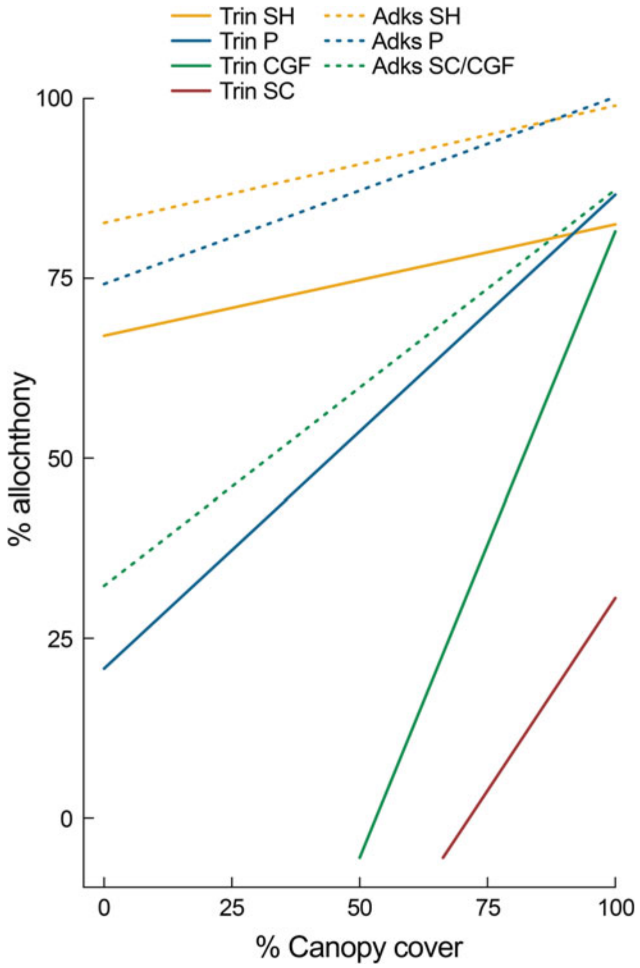

Fig. 9.11 The relationship between reliance on allochthonous energy inputs, determined from hydrogen isotope ratios of consumer organisms, and percent canopy cover differs between functional groups and between temperate and tropical sites. Tropical streams are more autochthonous than temperate streams, and tropical sites become autochthonous more rapidly with decreasing canopy cover. Functional group codes are as follows: SH = shredders, P = predators, CGF = collector gatherer/filterers, SC = scrapers. Solid lines represent data from tropical streams in Trinidad (Trin) and dashed lines represent data from temperate streams of the Adirondacks (Adks) in New York, US (Reproduced from Collins et al. 2016)

affecting basal resources. However, new tools based on energy assimilation make clear that flexible feeding habits, intermixing of energy sources of different origin, and differential assimilation can be important complications, not revealed using traditional methods solely relying on FFG classification and gut content analysis. Stable isotopes, fatty acid analyses, biomarkers and other emerging techniques will increasingly be the approaches most useful in revealing energy pathways in lotic ecosystems.

9.2 Trophic Roles of Lotic Fishes

Viewed across an assemblage of species, stream fishes consume virtually every resource available, and many individual species consume a wide range of resources, often changing diet over ontogeny and across environmental setting (Matthews 1998; Gelwick and McIntyre 2017). This makes trophic categorization understandably difficult, and there does not appear to be universal agreement on any single trophic classification in the literature. Regardless of these challenges, in virtually any study of fishes at a locale where one wishes to understand food web relationships and what determines the composition and relative abundance of species present, trophic categorization provides an important perspective. For convenience, we will begin with a discussion of these categories, and later review the caveats. Trophic categories can be as detailed as needed if one's objective is to describe differences in food consumed and feeding mode within a particular assemblage of species. To provide a general framework, however, the following categories have broad applicability: herbivores, detritivores, planktivores, omnivores, benthic invertivores, midwater-surface feeders (largely on insects), and piscivores. Where appropriate, one can add specialized categories such as snail-eaters, scale and fin eaters, fruit-eaters, parasites such as lampreys, and so on.

9.2.1 Fish Trophic Categories

Most fish species of temperate streams feed on invertebrates, which frequently make up much or virtually all of their diet. Aquatic invertebrate prey can be captured from the benthos, as individuals suspended in the water column, referred to as "drift", and as terrestrial infall on the water surface or entrained in the current. Invertivores thus can be separated into benthic feeders, mid-water feeders, and surface feeders. Benthic invertivores consume mainly aquatic insects, although crustaceans, mollusks, worms, and other invertebrate taxa also are eaten. Invertebrates in the water column are mostly aquatic insects dislodged from the benthos or present due to the phenomenon of drift, discussed further in Chap. 10. Some terrestrial invertebrates may be included in the diet of mid-water fishes, and may be an even more substantial fraction of the diet of surface feeders. Some studies have found it impractical to distinguish by feeding position, and simply refer to generalized invertivores. Aquatic insects and other invertebrates also comprise a significant portion of the diet of tropical stream fishes across most habitats, and terrestrial invertebrates often are important in smaller headwater streams of the tropics (Wolff et al. 2013; Ramírez et al. 2015).

Herbivory is not common among the stream fishes of North America, where only about 55 of over 700 total fish species are primarily herbivorous. Most macrophyte-eating fish are native to tropical waters, or to rivers in Asia or Europe (Matthews 1998), and some, including the grass carp *Ctenopharyngodon idella*, have been introduced into other regions for weed control. Grass carp daily rations (in wet mass of macrophyte tissue) range from 50% to over 100% of their body mass per day, indicating that this feeding strategy is based on processing a high volume of material. Grass carp also are known to have a low metabolic rate and assimilation efficiency relative to other fishes, and to require animal protein for proper growth. *Campostoma*, a cyprinid known as the stoneroller due to male nest-building behavior, is an important herbivore in many regions of the eastern to central United States, scraping algae from rocks and logs with the cartilaginous ridge on its lower jaw. In a small stream in Oklahoma, US, where the presence or absence of *Campostoma* was determined by either the distribution of its predator or by experimental manipulation, dense standing crops of attached algae (predominantly *Spirogyra* and *Rhizoclonium*) accumulated in areas lacking *Campostoma* but were scarce where the herbivore was present (Power et al. 1985).

Herbivorous fish species often make up a larger proportion of the total fish assemblage in tropical compared to temperate streams, where they can have strong effects on plant and animal abundances. Plant matter was a significant percentage (2–25%) of the diet of 77% of the 17 fish species in a Costa Rican stream (Wootton and Oemke 1992). Fish consumed a native grass, *Panicum*, leaves of two riparian plants *Ficus insipida* (a fig) and *Monstera* (a large-leaf member of the Araceae, often seen as a house plant), and periphyton, demonstrated by comparing loss of plant matter in locations exposed to fish, versus cage exclusions. Armored catfish (Loricariidae: Siluriformes) are an important group of grazing fishes, with 92 genera and at least 680 species occupying freshwater habitats of tropical and subtropical Central and South America (Delariva and Agostinho 2001). Noted for their dorsoventrally flattened body form, bony plates covering their bodies, and sucker-like mouths, loracariids are common algivores and detritivores in Neotropical streams, and also popular aquaria fish. Various species feed by scraping attached algae and diatoms from the substrate or by vacuuming up organic detritus, often including associated microorganisms. Armored catfish species also can differ in habitat use and substrates grazed. In streams of Panama, the most common loricariid, *Ancistrus*, grazed periphyton from flat surfaces on wood, bedrock, and clay substrates in pools, whereas others specialized in grazing on substrates such as pebbles in riffles (Power 1983). Herbivorous and detritivorous fish generally have large gut lengths relative to their body lengths (Delariva and Agostinho 2001; Ward-Campbell et al. 2005), facilitating prolonged digestive action by enzymes and microflora. Indeed, relative gut length is a good indicator of trophic position, distinguishing carnivores, with short guts, from herbivores and detritivores, with their elongated, coiled guts. A review of body length and gut length relationships in 71 fish species found that, for the same body length, species that include plant material in their diet, either exclusively (pure herbivores) or in significant proportions (omnivores with preference for plant material) had greater gut lengths than fishes that prey on other animals, including omnivores with preference for animal material, and carnivores (Karachle and Stergiou 2010).

As with herbivores, relatively few riverine fishes of the temperate zone are detritivores. In North America, some fishes that are often or predominantly detritivorous are abundant and widespread, include the river carpsucker *Carpiodes carpio* and white sucker *Catostomus commersonii* (Cypriniformes: Catostomidae), as well as the introduced European carp *Cyprinus carpio* (Cypriniformes: Cyprinidae). Special adaptations include a muscular stomach to grind food, an intestine with greatly increased absorptive surface due to elongation (up to 20 times body length) or elaborate mucosal folding, and protrusible jaws that allow the fish to suck in fine, flocculant detritus. Although the number of detritivorous fish species may be few, in some circumstances, including larger rivers and reservoirs, they can dominate assemblage biomass (Miranda et al. 2019). At least for catostomids, animal prey can be an important dietary component, and so whether they should be considered detritivores or omnivores may vary from study to study.

In the Neotropics, detritivorous fishes in the families Prochilodontidae and Curimatidae are important components of many South American river systems, comprising over 50% of community biomass in some regions (Bowen 1983). In Africa, detritus-feeding fishes are found in the Citharinidae, the Cyprinidae, and some of the Cichlidae. Unsurprisingly, detritivorous species are most abundant in habitats where detritus is a major resource, often the downstream depositional reaches of larger rivers, in floodplain lakes and backwaters, and during dry seasons as the availability of other food items decrease. Because of their high contribution to biomass, detritivorous fishes play an important role in food webs, linking carbon originating in detritus both to piscivorous fishes (Winemiller 2004) and human fishers (Bowen 1983).

Omnivory is common in riverine ecosystems, more so if all life stages of organisms are considered, and if occasional ingestion of a wider range of food items meets whatever threshold is deemed sufficient to be classified as an omnivore. For example, many invertivores occasionally consume larval fish, and many piscivores also consume invertebrate prey. Some primarily herbivorous fishes can be considered omnivores even though the majority of their diet is plant matter, because animal prey, detritus, and organic-rich sediments frequently are consumed as well; a similar statement could be made for many detritivorous fishes. The central stoneroller minnow *Campostoma anomalum*, which has been shown to strongly limit benthic algae (Power et al. 1985), derived the majority of its growth in a tallgrass prairie stream from consumption of algae (47%), followed by amorphous detritus (30%), animal matter (21%), and leaves (2%) (Evans-White et al. 2003). Owing to differential digestibility, an omnivore may derive more of its growth from the animal portion of its diet, even if it is a lower fraction by mass. For many species, omnivory is a manifestation of what is often referred to as flexible or generalist feeding, topics we shall discuss further below.

Planktivores are found primarily in larger rivers, backwaters, floodplain lakes, and reservoirs, where both phytoplankton and populations of mid-water animal prey such as small crustaceans and rotifers can develop. Zooplanktivores include filter feeders such as paddlefish (family Polyodontidae), a primitive fish of large rivers, and gizzard shad (*Dorosoma cepedianum*), a member of the herring family, that do not use vision; sight-feeding filter feeders such as the alewife (*Alosa pseudoharengus*); and sight-feeding particle feeders such as yellow perch (*Perca flavescens*). Many small-bodied fishes and younger stages of larger fishes are sight-feeding particle feeders. Prey selection is influenced by gill raker spacing in filter feeders, by prey visibility (positively influenced by prey size and negatively influenced by turbidity), and prey ability to escape buccal suction (Matthews 1998).

Two planktivorous species of Asian carp introduced into North America for aquaculture and control of algal blooms now are widespread throughout much of the Mississippi River system. Larvae of the silver carp (*Hypophthalmichthys molitrix*) feed principally on zooplankton, and adults feed primarily on phytoplankton and to a lesser extent also consume zooplankton and detritus. A highly specialized filter feeder, the silver carp exerts a strong current with its buccal cavity, has fused gill rakers capable of filtering particles as small as 4 µm, and an epibranchial organ that secretes mucus that assists in trapping small particles. The related bighead carp (*H. nobilis*) consumes larger particles than silver carp, including a greater proportion of zooplankton. In backwater lakes of the Illinois and Mississippi rivers, planktivorous fishes included three native species: bigmouth buffalo (*Ictiobus cyprinellus*), gizzard shad, and paddlefish (*Polyodon spathula*); and non-native bighead and silver carp (Sampson et al. 2009). The gizzard shad and both carps consumed mainly planktonic rotifers, crustacean zooplankton were the preferred prey of paddlefish, and bigmouth buffalo consumed both rotifers and crustacean zooplankton. Planktivores can be abundant in floodplain lakes of the tropics, where the larvae in the genus *Hypophthalmus* (Siluriformes:Pimilodidae) and *Plagioscion* (Perciformes:Sciaenidae) feed on zooplankton. Both are piscivorous as adults, and important food fish. In a limnetic region of the Paraná River, Brazil, larva of *H. oremaculatus* fed on small cladocerans and rotifers, and larger larvae of *P. squamosissimus* also consumed calanoid copepods (Da Silva and Bialetzki 2019). More surprisingly, some species of the genus of *Rhabdolichops* (Gymnotiformes, New World electric or knife fishes) are highly specialized planktivores occurring in deep, swift waters of the Orinoco River main channel, where they consume large numbers of very small planktonic Crustacea and insect larva (Lundberg et al. 1987). The terminal mouth, relatively large eye, and elongate and bony gill rakers of *R. zareti* are adaptations to planktivory that differentiate it from congeners.

Piscivores have a diet primarily or exclusively of other fish. For such a diet, the piscivore must have a size advantage over its potential prey (usually other young-of-the year fishes), either by being born earlier, being born at a larger size, or growing faster. Some species are piscivorous in their first year, some after age one, and some after more years of growth. Summarizing findings for 27 species of freshwater piscivores from Europe and North America. Mittelbach and Persson (1998) found that species that were born larger and had larger mouth gapes became piscivorous at younger ages and at smaller sizes. The size of prey eaten increased with predator size in all species, and prey sizes in the diets were remarkable similar for piscivores of similar body length despite morphological differences among piscivore species. Evidently, most of the variation in the sizes of prey consumed is due to differences in piscivore body size rather than among species. The number of predator species in any local assemblage varies, but systems with more prey fish species tend to have more piscivorous fish species, often by a factor of three to four (Matthews 1998).

The brown trout (*Salmo trutta*) is a good example of a facultative piscivore that transitions to a primarily piscivorous feeding mode at approximately 30 cm in length (Jensen et al. 2012), although it may consume fish before reaching this size. A detailed energy budget for brown trout found that energy intake, growth, and the optimum temperature for growth all increased markedly when trout changed their diet from invertebrates to fish, indicating significant benefits of shifting to a more energy-rich diet (Elliott and Hurley 2000).

Finally, some fish species exhibit unusual and highly specialized adaptations for feeding, although these specialists may be restricted to certain environments. The redear sunfish *Lepomis microlophus* (Centrarchidae), also called the shellcracker, has thick pharyngeal teeth that allow it to crush snails, its preferred food (Keast 1978). At least 200 species of frugivorous fishes are known from tropical South America, consuming fruit from flooded forest habitats during the high water season (Goulding 1980; Correa et al. 2007). Frugivores contribute a substantial fraction of the fishery harvest, and not incidentally serve as important seed dispersal agents (Anderson et al. 2009). Fruit-eating species of the Characidae possess multicuspid, molariform teeth able to crush hard seeds, whereas catfish swallow fruits and seeds whole. Several South American species are lepidophagous, or scale-eaters, including species of piranha (Serrasalmidae), and *Probolodus*, *Roeboides*, and *Roeboexodon* species of the Characiformes. Some scale-eaters will also feed on fins of other fishes, and many omnivorous or predatory fish may on occasion nip the fins of other fishes. A few African species in the family Distichodontidae are specialized fin-eaters, or pterygophagous. The neotropical knifefish *Hypostomus oculeus* (Gymnotiformes) has spoon-shaped teeth adapted for feeding on wood. Parasitic species include some lampreys, jawless fish of the order Petromyzontiformes that attach and bore into the flesh of other fishes to suck their blood and body fluids; and the candiru (*Vandellia cirrhosa*) in the catfish family Trichomycteridae. Native to the Amazon Basin and known as the vampire fish, the candiru feeds on blood and is commonly found in the gill cavities of other fishes; very occasionally, it invades human orifices of unclothed bathers.

9.2.2 Patterns in Fish Trophic Composition

Given this list of trophic categories, what can be said about the relative number of species occupying each feeding role? As we shall see, some patterns are rather general, but the trophic composition of fish assemblages varies with longitudinal position from headwaters to lowland river, between the temperate zone and the tropics, and with local differences in resource availability and habitat. Common changes in the species composition of stream fish assemblages along a river's length include replacement of species, an increase in overall species richness, and a preponderance of larger species downstream (Horwitz 1978; Schlosser 1987). In both temperate and tropical rivers, the trophic composition of fish assemblages also changes from headwaters to river mouth in accord with changing resource availability and habitat, approximately as posited by the river continuum concept. Goldstein and Meador (2004) classified 359 species of North American lotic freshwater fish into trophic categories based on mouth position, teeth, pharyngeal accessories, the ratio of gut length to body length, peritoneum color, and stomach morphology together with reported stomach contents. Cross-sorted by stream size, it is evident that invertivores comprise over half of the species list (54-75%) except in large rivers, per cent herbivores increases downstream, and detritivores are uncommon (Table 9.3). These results are broadly consistent with an earlier study of 15 river systems in the US (Horwitz 1978), in which over half of the species present were invertivores/insectivores, and the number of piscivorous species averaged about one-third of the number of invertivore species and less than one-fifth of the total. Planktivores were absent from headwaters, piscivores increased downstream, and fewer than 20% of the species subsisted on a diet of plant and detrital material. Similar findings were obtained from studies of trophic representation along several near-natural and regulated large rivers in Europe, the River Doubs in France and the Rivers Rhine and Meuse in the Netherlands (Aarts and Nienhuis 2003). The proportion of species feeding on benthic invertebrates and periphyton decreased towards the river mouth, while the proportion of zooplanktivorous and phytivorous species increased, and detritivorous species did not show a clear trend. The percentage of piscivorous species was fairly constant at around 15% in all zones. Comparing the freshwater fish assemblages of headwater streams from four continents (Europe, North America, Africa and South America), Ibañez et al. (2009) noted similarities in longitudinal patterns, including an increase in species richness, a decline in invertivores, and an increase in omnivores.

From these studies, it is evident that fish trophic composition in temperate streams indeed changes along a river's length. In addition, it is apparent that most species are insectivore/invertivores, omnivores often are the second most abundant group (but without a strict threshold for omnivory, this designation can vary among studies), piscivores are third, and only a few species occupy remaining

Table 9.3 Percent frequencies of fish species by trophic category and stream size for 359 North American fish species and life history stages. Some species have more than one trophic and stream size preference. Reproduced from Goldstein and Meador (2004)

Stream size category					
Trophic category	Small streams	Small rivers	Medium rivers	Large rivers	Variable
Herbivore	9.6	9.3	11.7	18.8	6.6
Planktivore	11.5	3.1	8.5	21.9	7.7
Detritivore	5.8	4.3	9.6	3.4	5.5
Invertivore	67.3	75.2	54.3	40.6	56.4
Carnivore	5.8	8.1	16.0	15.6	24.2

trophic categories. As further evidence, a trait analysis constructed for 88 species of riverine fishes in Europe (Logez et al. 2013) showed herbivory, planktivory, and parasitic feeding each represented by two species, detritivory by five, and piscivory by nine, but 24 species were considered omnivorous and 44 were considered insectivorous species.

One might expect a wider range of trophic categories in tropical than in temperate river systems, owing to the much higher species richness found in tropical rivers (Albert et al. 2011). From studies of Atlantic Rain Forest streams of Brazil, Abilhoa et al. (2011) reported that the fish fauna included 269 species belonging to 89 genera and 21 families, in which characins (tetras and relatives), loricariids (armored catfishes and relatives), trichomycterids (candirus), rivulids (killifishes), and poeciliids (guppies) were strongly dominant. Species richness at a given locale can be much higher in tropical than in temperate streams. Combining data from more than 800 stream localities in the temperate zone, Matthews (1998) concluded that few reported 30 or more species at a locality, 20 or more species was not uncommon for eastern North America, and fewer than ten often was reported for the more depauperate streams of the western US. In contrast, Flecker (1992) collected 55 species of fishes in a 500-m study reach of Río Las Marias, an Andean piedmont stream of Venezuela. From seine collections in various habitats (sand, rock, wood; river vs lagoon) of the Cinaruco River, a species rich, backwater and floodplain river located in Venezuela's plains region, Arrington et al. (2005) estimate that as many as 50 to 80 fish species occur per habitat type, while over 280 fish species are known from the system.

Unquestionably one finds a wider range of trophic categories in tropical relative to temperate streams, including more species of herbivores and detritivores, and more unusual specialists. This is especially apparent in large tropical rivers with extensive lateral floodplains, where lake and backwater habitats connect to the river during high water, and where much fish production occurs in seasonally inundated habitats (Welcomme 1979). Plant production and detritus of both autochthonous and allochthonous origin are of great importance in these systems; consequently there is a greater role for mud and detritus feeding (which often supports the greatest biomass of fish), and for predation (which often dominates species richness). The extensive flooded forests of the Amazon, known as várzea forest, make available a wide variety of food items including seeds, nuts, fruits, flowers, leaves, monkey feces, numerous terrestrial invertebrates and the occasional vertebrate (Goulding 1980).

However, invertivores tend to dominate in tropical streams just as they do in their temperate counterparts, especially in upper reaches. Additionally, differences between lower-order, forested streams and larger, higher-order rivers also have some patterns in common with temperate locations. In a study of forested tropical streams of the Bolivian Amazon, Ibañez et al. (2007) distinguished eight trophic guilds based on statistical clustering of gut contents. Eighteen of the 30 fish species consumed invertebrates, and were further sub-divided by aquatic, terrestrial, and generalist feeding habit. Diet specialization was observed at almost all trophic levels, except for the omnivore and piscivore feeding guilds, which the authors considered to be generalists. Similar results were obtained from a study of small forested streams of the Amazon basin, Bolivia (Pouilly et al. 2006). Diet analysis for 28 fish species identified seven detritivores, four algivores, two piscivores. and 15 invertivores (further divided into 6 generalist, three benthic, and six aquatic specialists) (Fig. 9.12). Invertivores dominated or co-dominated with detritivores at higher elevations, and the trophic composition was more diverse at lower elevation sites owing to an increase in the relative number of detritivore, algivore and piscivore species. A diet dendogram for 48 species from floodplain lakes in Bolivian Amazon provide an interesting comparison (Pouilly et al. 2003) (Fig. 9.13). More species of zooplanktivores and mud feeders were reported; piscivores also were more numerous, and sub-divided into carnivores to represent more exclusive consumption of other fish. Mud feeder, algivore, and piscivore species were considered to exhibit the most dietary and morphological specialization, relative to omnivores, invertivores, and zooplanktivores. Clearly, tropical rivers harbor more trophic diversity, the majority of fish species in most systems feed on invertebrates, and feeding roles that are uncommon in the temperate zone can be well represented in tropical river systems, especially in larger rivers with floodplain lakes and backwaters. Longitudinal changes in trophic representation in tropical river systems are thus broadly similar to what is reported from temperate rivers, with the important qualification that lowland rivers with their floodplain lakes usually have considerably more species of herbivores and detritivores, both uncommon in the temperate zone, as well as more species of piscivores. However, these patterns describe species richness, and can be quite different if expressed as biomass (e.g., Wolff et al. 2013). Owing to their large body size and the abundance of their resource base, detritivores and herbivores can make up a disproportionate share of the biomass at lowland river sites.

9.2.3 Feeding Mode and Morphology

The dominant mode of prey capture in teleost fishes is suction feeding, accomplished by expansion of the buccal cavity, causing water and prey items to flow into the predator's mouth (Lauder 1980; Liem 1980). Some species have evolved more complex skull linkages capable of greater

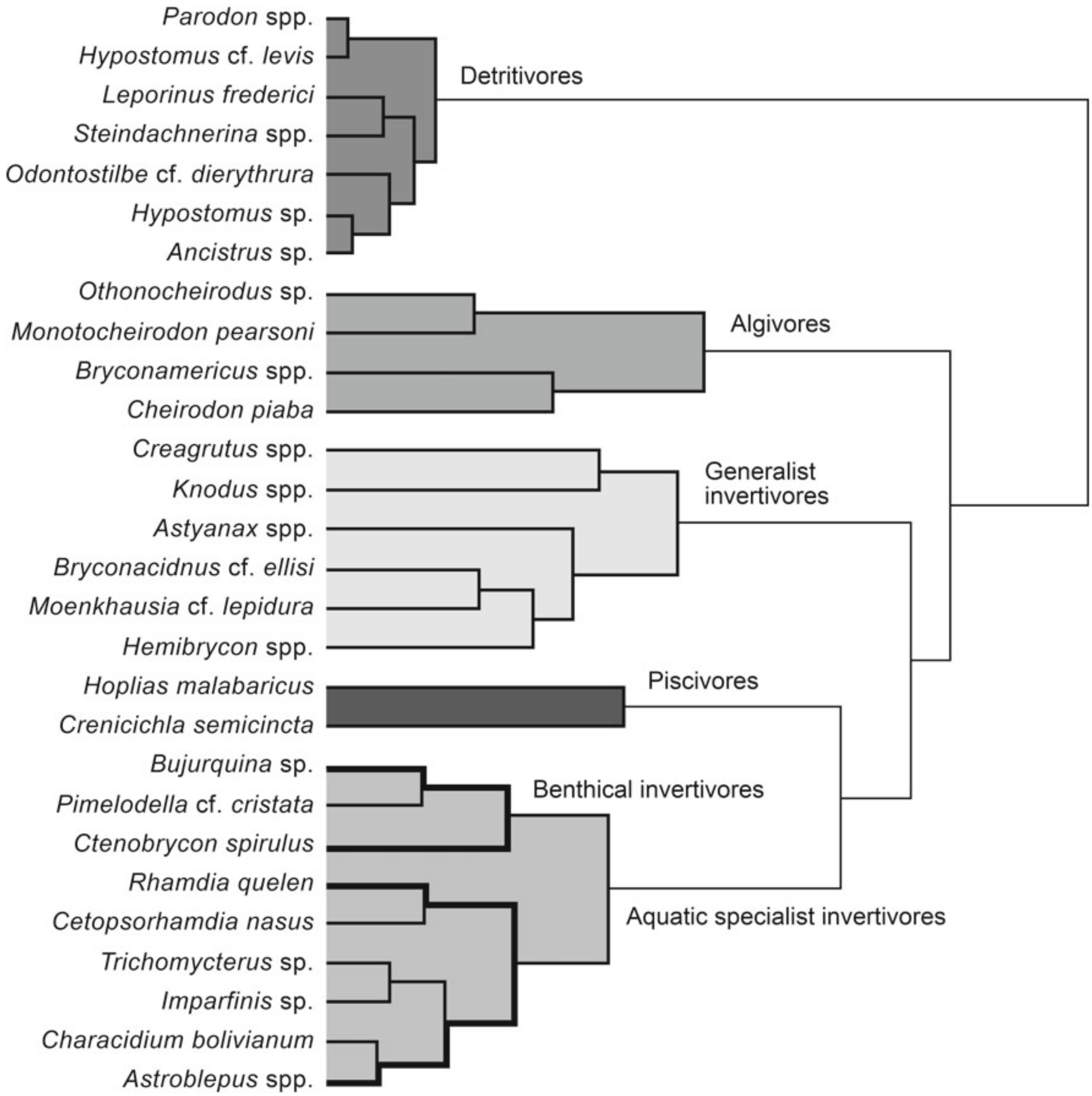

Fig. 9.12 Diet dendogram depicting trophic roles for 28 species of fishes from forested headwater streams in Bolivia (Reproduced from Pouilly et al. 2006)

suction force, and some combine suction feeding with forward body movement in a rapid strike during prey capture, referred to as ram suction. Some species grip prey in their jaws during capture, to manipulate, shred, or crush their prey. Wainwright and Richard (1995) showed that a functional analysis of lever distances and their ratios involved in opening versus closing the jaw could discriminate species that use ram-suction feeding versus biting or manipulation of prey. The jaw-lever systems for mouth opening and closing represent direct trade-offs for speed and force of jaw movement.

Various aspects of fish morphology have been found useful in understanding habitat and feeding preferences of fishes, as described in listings of fish traits (Frimpong and Angermeier 2010). Variation in body size, mouth gape and position, dentition, and gut length are frequently found to be strongly associated with feeding role, as well as visual and chemosensory adaptations. Traits associated with speed and maneuverability, including body shape and fin position, may influence both habitat use and prey capture. In a pioneering study of the relationship between fishes' ecological role and their morphological adaptations, Gatz (1979) examined 56 morphological features of 44 species seined from North Carolina piedmont streams, calculated 3,080 pairwise correlation coefficients among characters, and then used factor analysis to look for associations among characters in the correlation matrix. The first factor separated "lie-in-wait" biting predators from cruising suction feeders, the second

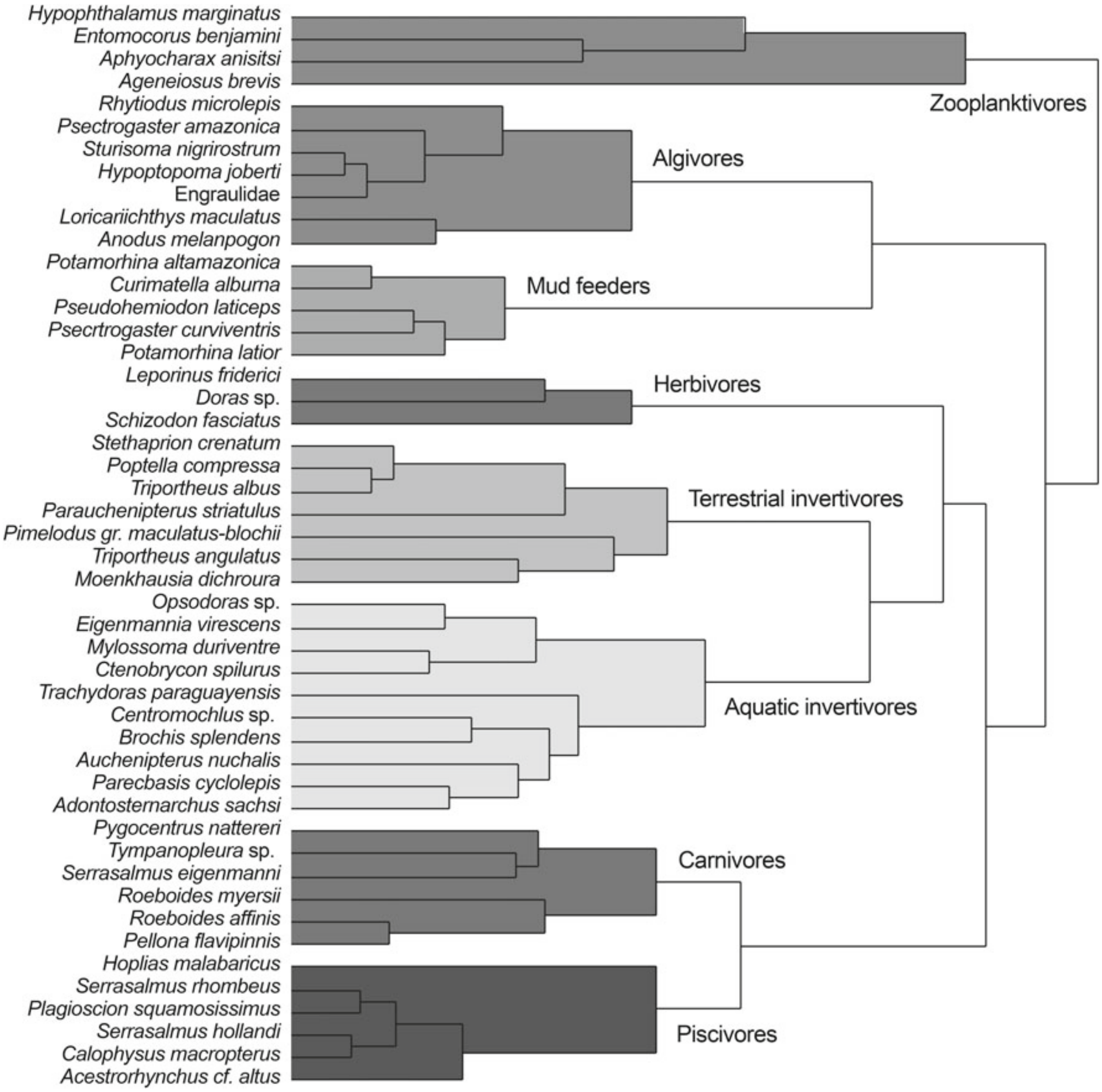

Fig. 9.13 Diet dendogram depicting trophic roles for 42 species of fishes from a low elevation floodplain site in Bolivia. (Reproduced from Pouilly et al. 2003)

reflected the differences in body shape and proportions associated with habitat use, the third factor separated a benthic from mid-water lifestyle, and the fourth separated small insectivores with short guts from other fishes. Fishes with flat, deep bodies were associated with slow water habitats. Fishes with ventral mouths obtained relatively more food from the bottom, those with terminal or anterior mouths did not. Fishes that dwell on or near the bottom in fast water regions had reduced swim bladder volume, and relative gut length was greatest in mud feeders, to list some principal findings.

Many subsequent investigations of what is known as the study of ecomorphology provide further evidence that fish trophic position often accords with their morphological adaptations. Among eleven species of characid fishes collected from streams in Rio Grande do Sul, Brazil, those whose mouth positions were sub-terminal fed mainly on benthic items such as detritus, organic matter, and benthic aquatic insects (Bonato et al. 2017). *Bryconamericus* is an example, feeding in a head-down position, applying lips and teeth to the substrate to feed by rasping and suction. In contrast, species of *Astyanax* have the mouth in a more superior position, permitting them to forage from the surface and water column on floating terrestrial insects. The angle of their teeth is best suited for biting and tearing plants and ingesting terrestrial insects. Piscivores often are distinguished by their greater mouth gape, longer lower jaws and tooth size, an upturned mouth, and greater snout length. These features describe the characin genus *Oligosarcus*, which feeds primarily on other species of fish. Armored catfish are another example of highly specialized feeding morphology. A study of six species occurring in the Upper Paraná River, Brazil, revealed species adapted for both suction and scraping feeding modes (Delariva and Agostinho 2001) (Fig. 9.14). Species that feed on fine grained detritus obtain food by suction, and possess a well-developed respiratory membrane, long gill rakers, rudimentary labial and pharyngeal teeth, a thin stomach wall, and a long intestine. In comparison, species feeding on periphyton by scraping the substratum have large, strong, spatulate teeth, short gill rakers, a well-developed stomach, and a shorter intestine. Of the six species studied, one (*Rhinelepis aspera*) was clearly a suction feeder, two (*Hypostomus microstomus* and *Megalancistrus aculeatus*) were scrapers, and others (*Hypostomus regani, H. ternetzi, H. margaritifer*) were intermediate.

An important sub-theme in the study of ecomorphology concerns the extent of morphological convergence between unrelated species that occupy essentially the same trophic role. Unquestionably this occurs, as attested to by similarities in body form and jaw structure among unrelated piscivores, in the greater gut length of herbivores and detritivores compared with invertivores and piscivores, and so on. A comparative study of 30 ecomorphological traits assessed for the dominant fish species from lowland stream and backwater sites in Alaska, temperate North America, Central America, South America, and Africa found numerous ecomorphological convergences and identified several cases of ecologically equivalent species, despite dominance by different orders of fish within the different biotic regions (Winemiller 1991) (Fig. 9.15). When an ecomorphological analysis is applied to a local fish assemblage, however, one frequently encounters multiple species within the same genus or family, with the consequence that when certain similarities are found in morphology and feeding habit, common ancestry may be the more robust explanation. In an early demonstration of the confounding influence of phylogenetic relatedness, Douglas and Matthews (1992) found that ecomorphological analysis of 17 species of fish from the Roanoke River and its tributaries simply confirmed that trophic ecology frequently conformed to family-level taxonomy. However, morphological variation within eight

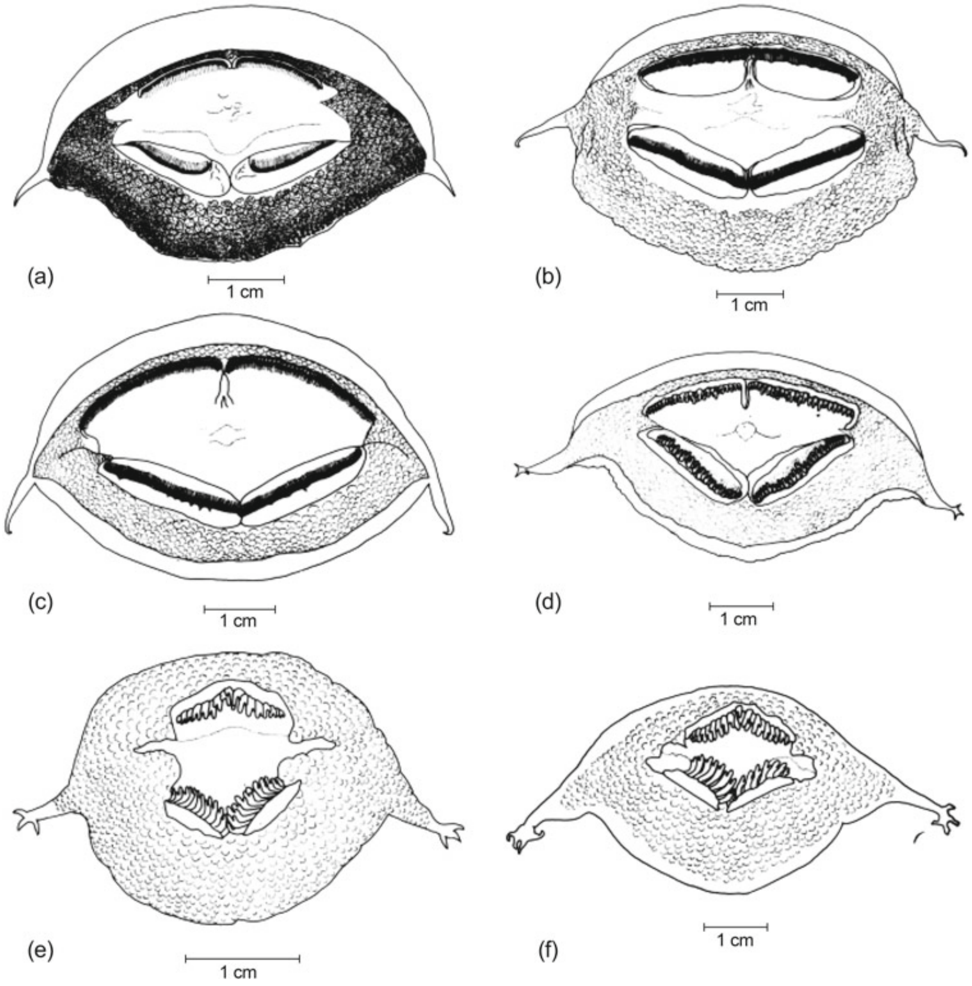

Fig. 9.14 Ventral view of the position and form of mouth for six loricariids collected from the Upper Paraná River, southern Brazil. (**a**) *Rhinelepis aspera*; (**b**) *Hypostomus regani*; (**c**) *H. ternetzi*; (**d**) *H. margaritifer*; (**e**) *H. microstomus*; (**f**) *Megalancistrus aculeatus*. *R. aspera* feeds on fine grained detritus using suction to obtain food, and has rudimentary labial and pharyngeal teeth. *M. aculeatus* and *H. microstomus* feed on coarser material such as periphyton by scraping the substrate, and possess large, strong, spatulate teeth. The remaining species are intermediate (Reproduced from Delariva and Agostinho 2001)

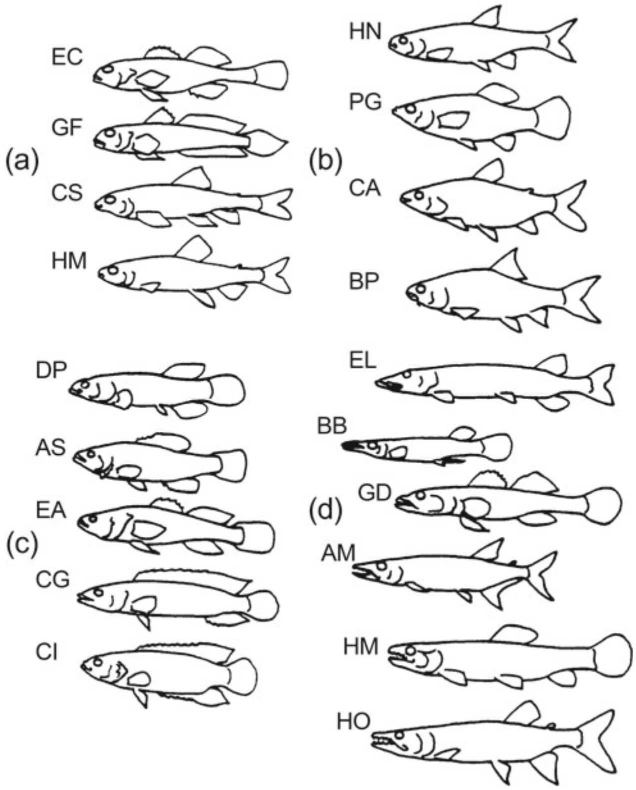

Fig. 9.15 Examples of ecomorphological convergences among fishes of five study regions. Note that fishes are not drawn to the same scale. (**a**) Small, benthic invertebrate-feeders: ED = *Etheostoma chlorosomum* (Perciformes, Percidae; North America), GF = *Gobionellus fasciatus* (Perciformes, Gobiidae; coastal Central America), CS = *Characidium* sp. (Characiformes, Characidiidae; South America), HM = *Hemigrammocharax multifaciatus* (Characiformes, Citharinidae; Africa). (**b**) Small, epibenthic algivores/detritivores with long, coiled guts: HN = *Hybognathus nuchalis* (Cypriniformes, Cyprinidae; North America), PG = *Poecilia gilli* (Cyprinodontiformes, Poeciliidae; Central America), CA = *Steindachnerina* (= *Curimata*) *argentea* (Characiformes, Curimatidae; South America), BP = *Barbus poechi* (Cyrpiniformes, Cyprinidae; Africa). (**c**) Small, cylindrical, vegetation-dwelling invertebrate-feeders: DP = *Dallia pectoralis* (Salmoniformes, Umbridae; Alaska), AS = *Asphredoderus sayanus* (Percopsiformes, Asphredoderidae; North America), EA = *Eleotris amblyopsis* (Perciformes, Eleotridae; Central America), CG = *Crenicichla geayi* (Perciformes, Cichlidae; South America), CI = *Ctenopoma intermedium* (Perciformes, Anabantidae; Africa). (**d**) Fusiform, sit-and-wait/stealth piscivores: EL = *Esox lucius* (Salmoniformes, Esocidae; Alaska), BB = *Belonesox belizanus* (Cyrpinodontiformes, Poeciilidae; Central America), GD = *Gobiomorus dormitor* (Perciformes, Eleotridae; Central America), AM = *Acestrorhynchus microlepis* (Characiformes, Characidae; South America), HM = *Hoplias malabaricus* (Characiformes, Erythrinidae; South America), HO = *Hepsetus odoe* (Characiformes, Hepsetidae; Africa) (Reproduced from Winemiller 1991)

species of minnow (Cyprinidae) did have some power in predicting microhabitat use.

Because similarities between diet and morphology within a fish assemblage can be simply the consequence of shared phylogeny, some authors have found ways to address this. Using a statistic of taxonomic relatedness to factor out this influence, Ibañez et al. (2007) were able to show that relative intestinal length, standard length, and mouth orientation indeed discriminated among some trophic guilds within an assemblage of 30 fish species from forested tropical streams of the Bolivian Amazon. Fishes belonging to the algivorous and detritivorous guilds had large relative gut lengths. Benthic fishes from the algivorous and mud feeder guilds also exhibited relatively narrow heads and a ventral (Loricariidae) or oblique (Curimatidae) mouth orientation. Small size characterized most fishes of the aquatic invertivorous guild, whereas members of herbivorous and piscivorous guilds tended to be larger. However, although species having similar diet showed some similarity in morphological attributes, Ibañez et al. (2007) point out that this link was rather weak, discriminating among the three trophic guilds just mentioned but not others. A study of fishes inhabiting small streams of the Colombian Amazon also provided mixed evidence for a correspondence between morphology and diet (Ramírez et al. 2015). Several fish species feeding on aquatic invertebrates had multicuspid teeth, but so did a seed-eating species. Two species of knifefishes both had a long coiled intestine, but one was an omnivore, feeding mostly on fish and aquatic invertebrates, and the other an herbivore. However, tooth adaptations did relate to diet: the former has bi-cuspid teeth for invertebrate feeding, the latter has spoon-shaped teeth adapted for feeding on wood.

Although it is generally true that predators are larger than their prey, the largest species in an assemblage may not be predators. Because primary consumer fish species (algivores and detritivores) exhibited a wide size range in a diverse tropical food web in a savannah tributary of the Orinoco River, Venezuela, predatory fishes of all body sizes are able to exploit taxa low on the food web, resulting in relatively short, size-structured food chains for individual components of the overall web (Layman et al. 2005).

In addition to the morphological specializations just described, the sensory systems of fishes can be finely attuned to environmental constraints on food acquisition. Light level differs between day and night, with depth, and with the dissolved and suspended load, creating markedly different visual environments for seeking and capturing prey. River water varies in clarity, perhaps nowhere more evidently than in the Amazon basin. Whitewater streams are heavily colored by their alluvial loads, while blackwaters carry little silt but are darkly stained with dissolved material. Typical Secchi disk (water clarity) readings are less than 0.2 m in the former, 1–1.5 m in the latter (Muntz 1982). Clearwater rivers carry comparatively little silt or dissolved organics, and light penetration often equals or exceeds 4 m. Absorbance of short-wavelength light is relatively great in fresh water, and more so as light penetration is reduced. Levine and MacNichol (1979) examined 43 species of mostly tropical freshwater fishes, dividing them into four groups on the basis of visual pigments. Species with strongly "short-wave-shifted" visual pigments were primarily diurnal, and fed from the surface or in shallow waters. Several species exhibiting the typical behavioral and morphological characteristics of catfishes lay at the other extreme. Their visual pigments were the most long-wave sensitive; in addition they were primarily benthic and probably foraged either nocturnally or in very turbid waters.

Of several environmental variables considered to influence fish assemblage structure in floodplain lakes of the Orinoco River, Venezuela, transparency was a remarkably reliable predictor of species composition, including the numerical density of piscivorous species (Rodríguez and Lewis 1997). Fish with sensory adaptations to low light were dominant in turbid conditions (Secchi transparency <20 cm), whereas visually oriented fishes predominated in clear lakes (Secchi transparency >20 cm) but declined seasonally, concomitant with a decline in transparency. Species of characiforms, cichlids, and clupeomorphs that usually are diurnal and rely on vision were most abundant in clear floodplain lakes, including the peacock bass, *Cichla orinocensis*, and pike-like characiforms species *Acestrorhynchus microlepis*, *A. nasutus*, and *Boulengerella lucia* that lunge and engulf their prey. Catfishes, knifefishes, and a piscivorous sciaenid were most abundant in turbid lakes. Catfishes and knifefishes are primarily nocturnal, foraging efficiently in turbid waters using tactile and chemical sensors in catfishes, and electric sensors in knifefishes, while also gaining refuge from visual predators.

9.2.4 Challenges of Fish Trophic Categorization

As mentioned earlier, the use of fish trophic categories requires important caveats. Many species change their diet as they transition through life stages and grow in size. Such ontogenetic changes are especially well known in many piscivores, which may be invertivores as larvae, generalists or omnivores during the first one or more years of growth, and primarily piscivorous once a certain size threshold is reached. This challenge can be met at least in part by restricting trophic classification to adult individuals, or through the use of "ecological species", in which different life stages of the same taxonomic species are assigned to different trophic categories. A second issue involves habitat use, which can change, for example, with water level between wet and dry seasons, or when risk of predation forces an organism into less preferred locations with possibly different resource availability. Species that can occupy a wide range of habitats likely encounter a wider range of resources. Confronted with a variable and fluctuating resource base, the ability to feed opportunistically on different types of food is advantageous. While it is difficult to operationally define a generalist versus a specialist, one can intuitively grasp that for some species it may be advantageous to be able to eat a broad diet, and others may be more successful by being the best at eating just one thing. Even in the tropics, where some wonderful examples of ecological specialization can be found, many observers have opined that a generalist or opportunistic feeding strategy seems to characterize the majority of species (Lowe-McConnell 1987; Ibañez et al. 2007; Mortillaro et al. 2015). It is not uncommon for the same species to be found to feed quite differently in separate studies. In the Apure and Arauca rivers, two tributaries of the Orinoco River, the catfish *Pseudoplatystoma hemioliopterus* is primarily piscivorous, while in the Amazon basin, fruits and seeds have been found in their stomachs (Barbarino Duque and Winemiller 2003). Goulding (1980) reported that piranhas ingested mostly seeds and fruit during the flooded period.

Traditional studies of dietary analysis of gut contents are increasingly being supplemented by recently developed methods relying on analyses of stable isotopes and fatty acids. These hold considerable promise for identifying not only what species eat, but what food resources are important to assimilation and growth, both for individual species and the entire food web. Employing these methods to study food source utilization by nine fish species from two Amazon floodplains near the confluence of the Solimões and Negro rivers, Mortillaro et al. (2015) reported wide-ranging diets and feeding flexibility. Detritivores were positioned at the base of the food chain as expected, but fatty acid analysis pointed to inclusion of a high-quality food source, such as microalgae, in their diets. Both omnivores and insectivores exhibited opportunist feeding behavior, consuming a wide range of food resources. Piscivores had the most ^{15}N-enriched signature, consistent with their position at the top of the trophic chain. Only one herbivore, *Schizodon fasciatus*, consumed C4 macrophytes, which suggested some digestive specialization to cope with their low digestibility. While the diet of most species was broadly consistent with their trophic designation, results showed considerable dietary flexibility, differences in diet between the same species at different locations, and the ability of species to adapt their feeding behavior to changes in resource availability driven by hydrologic seasonality.

In summary, trophic categorization of fishes has its uses and its limitations. Different feeding roles can be identified within an assemblage of fishes based on differences in diet, feeding behavior, and morphology. What is also evident, however, is that across life stages, habitats, and seasons, many species are flexible in their diet, benefiting from their ability to exploit different food items based on changing availability of resources. Thus, studies often refer to the high frequency of dietary plasticity, or characterize many of the species present as omnivorous, generalists, or opportunists. It also is important to recognize that habitat, enemies, disturbance frequency, and many other environmental variables influence where a species occurs, and very likely the range of food resources. In practice, trophic categories are a useful way to summarize the broad similarities in the feeding ecology of taxa that have similar feeding roles, as long as their use doesn't obscure the individual differences and great flexibility of which fish are capable.

9.3 Other Vertebrates

Although fishes are the principal vertebrate component of most riverine food webs, all vertebrate classes have representatives in running waters. In small headwater streams, salamanders and snakes may be important top predators; there are many species of fish-eating birds, and some that consume aquatic invertebrates; a few mammals feed primarily or exclusively on aquatic prey, and a surprising diversity of mammals do so at least occasionally. Although many of these species consume animal prey, algal, higher plant, and detrital resources are consumed as well. Especially in larger rivers, the littoral zone and floodplain habitats provide feeding opportunities across all trophic levels for vertebrate consumers.

Larval amphibians in the temperate zone are found primarily in standing waters, but they can be diverse and abundant in tropical streams. The majority rasp algae and detritus from substrates and so are herbivores and detritivores, although unknown amounts of microbes and small organisms likely are ingested as well, suggesting a more omnivorous diet. Based on fatty acid analysis, anuran tadpoles sampled from ponds in Illinois, US, consumed larval insects and phytoplankton at one site and mainly periphyton along with sediments at another site, apparently reflecting predominant resource availability (Whiles et al. 2010). Larvae of the web-footed frog, *Rana palmipes*, are widely distributed in Neotropical streams, where they are epibenthic consumers of algae and sediments. Using cage enclosures with a range of densities, Flecker et al. (1999) observed rapid accumulation of benthic sediments when tadpole density was low, but rapid removal of sediments at higher tadpole densities. In addition, tadpole growth was strongly related to sediment supply. Herbivorous and detritivorous amphibian larvae likely obtain some nutrition from occasional ingestion of animal prey, as Schiesari et al. (2009) reported from stable isotope analysis of four ranid species from US wetlands. Amphibian declines have been reported throughout the world in recent decades, often attributed to *Batrachochytrium dendrobatidis*, an amphibian-specific aquatic fungus. Significant declines of larval amphibians in upland streams of the Neotropics have resulted in increased biomass and production of both algae and invertebrate algal grazers (Colón-Gaud et al. 2009), strongly indicting that tadpoles at their pre-decline abundance reduced the amount of algal primary production available to other consumers.

Salamanders prey upon invertebrates, other amphibians, and fish, and may be the principal vertebrate predators in some headwater streams. Petranka (1984) concluded that the larval two-lined salamander *Eurycea bislineata* was an opportunistic generalist, consuming a variety of insect larvae and crustaceans. Salamanders can attain large size, including *Megalobatrachus* of the Orient, *Cryptobranchus* (the hellbender) and *Necturus* (the mud puppy) of eastern North America, and *Dicamptodon ensatus* of the Pacific Northwest of North America. Using suction feeding, adult hellbenders consume primarily crayfish and fish, but larvae consume mainly invertebrate prey such as mayflies and caddisflies, shifting to larger prey at later life stage (Hecht et al. 2017).

Reptiles that feed in rivers include many families of snakes but especially the Colubridae (water snakes), turtles, alligators, and crocodiles. Turtles are, for the most part, omnivores of sluggish streams and rivers, consuming substantial amounts of invertebrate and fish prey, but some are more specialized as herbivores or carnivores. Snakes and members of the Crocodilia are predators of fish and invertebrates in aquatic environments, but often consume other vertebrates as well. Size of prey relative to size of predator is a common constraint, and many predators increase the size and breadth of their diet as they grow.

Piscivory in snakes has evolved independently in multiple lineages, attracting study of the different behavioral and mechanical solutions to the problem of feeding in water. In a number of species, prey capture is accomplished by a sideways head-sweeping motion to minimize drag on the skull and/or to avoid pushing prey items away from the mouth. However, some aquatic species of garter snakes (*Thamnophis*) have been reported to use fast forward strikes to capture fish and amphibians. Filmed attacks by two species of aquatic piscivorous garter snakes established that they oriented visually toward prey items and struck forward rapidly with peak head velocities that approached speeds attained by fast striking species on land (Alfaro 2002). The dice snake *Natrix tessellate* (Colubridae), widely distributed in Europe and Asia, also uses frontal strikes to capture prey underwater. Aquatic species in the natricine sub-family include primarily piscivorous species with narrow, streamlined heads, and species that prey mainly on frogs and have broader heads, evidently reflecting the antagonistic design requirements of fast underwater striking versus the consumption of bulky prey (Brecko et al. 2011).

Diet studies indicate that aquatic snakes are generalist predators, consuming a wide range of fish, amphibian, and other prey, with some specializing more on fish and others on amphibians. An aquatic population of the Oregon garter snake *T. atratus* fed on small prey along the stream margin as juveniles, but as adults they consumed a wider variety of prey types and sizes, especially concentrating on larvae of the Pacific giant salamander in mid-stream substrates (Lind and Welsh 1994). By palpating the abdomen of *N. tessellata* captured from streams of the Tolfa Mountains, Italy, to induce regurgitation of ingested food, Luiselli et al. (2007) observed that fishes accounted for over 90% of the diet, and anurans the remainder. Larger individuals had a broader diet, including prey species that were never consumed by juveniles. Prey were primarily diurnal, as is this sit-and-wait predator, and the most abundant prey species were also the most frequently consumed. A review of the feeding habits of this well-studied snake reported a total of 113 prey taxa, mostly fish, but invertebrates, amphibians, reptiles and mammals were also eaten (Weiperth et al. 2014). Environmental setting plays a role, as non-fish prey were especially important in deserts, high mountains, and in dry Mediterranean areas. Reports for other species of aquatic snakes also suggest generalist and opportunistic feeding. From stomach analysis of museum specimens of three species of Amazonian water snakes in the genus *Helicops* (Colubridae), de Carvalho et al. (2017) recorded 36 species of fishes and 11 species of anurans. All fishes found in snake guts occupy middle and upper layers of water column and are primarily nocturnal, as are these snakes.

Members of four families of turtles in the sub-order Cryptodira may be found in aquatic habitats, including species of the Emydidae (e.g., Blanding's and painted turtles), Kinosternidae (mud and musk turtles), Trionychidae (soft-shell turtles) and Chelydridae (snapping turtles). Most can be described as carnivorous or omnivorous, although some also consume plant matter. In addition, two families in the sub-order Pleurodira, the Podocnemidae and the Chelidae (side-necked turtles) occur in freshwater habitats in the Southern Hemisphere. The Podocnemidae are also primarily carnivorous. The Chelidae include snake-necked species that mainly are predators of fish, invertebrates, and gastropods; and short-necked forms that are largely herbivorous or molluscivorous, but include several species that primarily eat fruits.

North American species of Emydidae have been reported to have a substantial component of plant matter in their diet. The Ouachita map turtle, *Graptemys ouachitensis,* of the Mississippi River consumes mostly animal prey when small, but plant matter becomes more important with increase in size, including fruits, seeds, leaves, and grasses (Moll 1976). The painted turtle *Chrysemys picta* is considered an omnivorous generalist whose diet includes algae, vascular plants, aquatic invertebrates, insects, and vertebrates such as fish and frogs (Hofmeister et al. 2013). Two widely distributed South American turtles in the Podocnemidae, the yellow-spotted river turtle (*Podocnemis unifilis*) and the South American river turtle (*P. expansa*) both are primarily herbivorous, although accidental consumption of small animals may contribute important nutrition as well (Lara et al. 2012). Large-bodied species are thought to become increasingly herbivorous as they grow, presumably due to reduced prey capture ability as size increases.

As mentioned above, snake-necked and short-necked species of the Chelidae exhibit markedly different morphological and dietary specializations. Using stomach lavage, Tucker et al. (2011) compared the diets of three chelid species from free-flowing and impounded rivers in southeastern Queensland, Australia. The white-throated snapping turtle *Elseya albagula* was primarily herbivorous, consuming fruits and plant matter; the saw-shelled turtle *Myuchelys latisternum* was a carnivore, consuming insects and crustaceans, but also some fruit and plant matter; and the Australian short-necked turtle *Emydura krefftii* was an omnivore, consuming algae, sponges, fruit and plant matter, as well as insects, snails, and crustaceans.

While some turtles clearly are primarily herbivorous and others, like the snapping turtle *Chelydra serpentina* (Chelydridae) of North America and its massive relative, the alligator snapping turtle *Macrochelys temminckii* of the southeastern US, are strongly carnivorous, omnivory is widespread in most freshwater turtle lineages. Even *C. serpentina* with its powerful jaws consumes plant as well as animal matter, and both scavenges and actively preys upon anything it can capture and swallow. However, the alligator snapping turtle is almost entirely carnivorous, often feeding by opening its mouth to reveal its tongue as a lure to an unwary fish.

American alligators (*Alligator mississippiensis*), the dominant apex predator across many aquatic ecosystems of the southeast US, are considered to be generalist predators. A compilation of data from a large number of studies of alligator stomach contents noted that prey included crustaceans, mollusks, fishes, amphibians, reptiles, mammals, birds, aquatic and terrestrial insects, and seeds (Rosenblatt et al. 2015). Analyzing the diet of over 200 individuals, Rosenblatt et al. established that diet contents varied with alligator size, capture location, and season. Although alligators are dietary generalists as a species, individual animals showed considerable specialization. Likely causes are habitat heterogeneity, with associated differences in prey composition, and the relative abundance and ease of capture of prey present.

At least 11 orders of birds make use of rivers and streams as feeding habitat (Hynes 1970). Many are fish predators but some feed directly on invertebrates (e.g. the Cinclidae or dippers, Ormerod 1985). The American dipper *Cinclus mexicanus*, found in western North America, forages mostly in fast-flowing streams where it feeds on aquatic insects, as well as small fish, fish eggs, and flying insects. Dippers plunge underwater to capture prey, returning to the surface to swallow their prey (Kingery and Willson 2019). Other species of birds are underwater hunters. The snake bird *Anhinga anhinga* stalks its prey underwater, spearing it with a rapid strike before returning to the surface; prey are then swallowed head first. The anhinga's diet includes many different species of small to medium-size fishes as well as invertebrates, snakes, and small turtles (Frederick and Siegel-Causey 2000). The common merganser *Mergus merganser* is an underwater pursuit predator with a slender and serrated bill for grasping prey. Its diet is primarily small fish, but also includes aquatic invertebrates, frogs, small mammals, birds, and plants (Pearce et al. 2015). Examples of aerial hunters include kingfishers, terns, and the osprey. The belted kingfisher *Megaceryle alcyon* preys on fishes near the surface to a maximum depth of about 60 cm, favoring clear water locations for best visibility, and capturing most prey at the surface without submerging (Kelly et al. 2009). Returning to its perch, the bird pounds its prey to stun it before swallowing head first. The least tern *Sternula antillarum* is found along major interior rivers of North America, feeding primarily on small fishes, with over 50 fish species listed as prey, and occasionally on invertebrates (Thompson et al. 2011). Terns fly or hover 1–10 m above water while searching for prey, then plunge-dive and grasp prey with open mandibles without fully submerging. The osprey *Pandion haliaetus* is the only North American raptor that consumes live fish as its main prey source, diving feet first to capture prey from within only about the top meter of water (Bierregaard et al. 2016). Prey typically are 10–30% but may be over 50% of the osprey's body mass, requiring powerful wing strokes for the partially submerged osprey to regain the air. The great blue heron *Ardea herodias* is one of the most prominent wading birds of North and Central America (Vennesland and Butler 2011). Individuals hunt by slowly wading or standing in wait in shallow water, but also will dive feet first after prey. Prey are caught by a rapid forward thrust of the neck and head, and most prey are swallowed whole. They have a broad diet, including fish, insects, mammals, amphibians, birds, and crustaceans. Aerial life stages of aquatic insects are prey for a number of insectivorous birds. The bank swallow *Riparia riparia* is an aerial feeder over aquatic and meadow habitats, consuming a wide variety of aquatic and terrestrial insects including mayflies, dipterans, and odonates (Garrison 1999). Diving ducks consume plant matter and a variety of invertebrates, and some such as the mergansers are specialized piscivores. Non-diving (dabbling) ducks primarily consume aquatic vegetation, but invertebrates such as snails attached to vegetation are also eaten.

While there is some evidence that avian piscivores do not have a major impact on fish populations except when fish are easily captured, such as during low water conditions (Draulans 1988), in some instances bird predation can significantly influence behavior or abundance of their prey. Steinmetz et al. (2003) altered the abundance of great blue herons and belted kingfishers along an Illinois prairie stream by suspending plastic bird netting along an exclusion reach and adding kingfisher perches along an augmentation reach. The mean sizes of two abundant prey, striped shiners and central stonerollers, decreased under normal and elevated predation but increased in the reduced predation reach, in accord with preferred prey sizes of the two predators, apparently due to a combination of direct mortality and prey emigration. Armored catfish in Panamanian streams experience significant predation risk from fishing birds (Power 1984), and this causes larger individuals to avoid shallow waters. Because these fish are effective herbivores, the depth distribution of periphyton inversely mirrors the distribution of fish.

A variety of mammals feed within river systems. Taxa ranging from shrews to racoons to bears occasionally or frequently consume invertebrates and fish, while muskrats, beaver, and the South American capybara consume aquatic and riparian vegetation. The European river otter *Lutra lutra* is primarily piscivorous in temperate European localities, whereas Mediterranean otters behave as more generalist predators, relying less on fish and more on aquatic invertebrates and reptiles (Clavero et al. 2003). Sedges and grasses are important dietary items for muskrats *Ondatra zibethicus* of North America and the capybara (*Hydrochoerus hydrochaeris*) of South America, two rodents capable of digesting this high-fiber diet. The capybara, the world's largest rodent, processes its high-fiber diet by a combination of hind-gut fermentation and re-ingesting its feces. Very large river-dwelling mammals include the plant-eating manatees of Central and South America and West Africa, and dolphins, which feed on invertebrates and fish. River dolphins are top predators and those from the Amazon have been found to eat at least 50 fish species from 19 families, including individuals up to 0.8 m in length (Best and da Silva 1984); in addition, they occasionally consume mollusks, crustaceans, and turtles. Fish consumption by dolphins is perceived as a conflict by at least some indigenous fishers, and there is evidence of intentional killings of the freshwater dolphins *Inia geoffrensis* and *Sotalia fluviatilis* in areas of the Western Brazilian Amazon (Loch et al. 2009).

Seasonal fluxes of anadromous fishes into rivers provide nourishment for a great many mammal species (Willson and Halupka 1995). Stable-isotope analysis of hair samples from 13 brown bear (*Ursus arctos*) populations located over a wide area of western North America identified populations ranging from largely vegetarian to largely carnivorous, and food resources ranged from mostly terrestrial to mostly salmon (Hilderbrand et al. 1999). The proportion of meat in the diet was strongly correlated with female body mass and litter size, and salmon was the most important source of meat for the most productive populations.

A few species of bats have become aquatic carnivores despite their ancestry as terrestrial invertivores. The greater bulldog bat *Noctilio leporinus* (Noctilionidae) of Central and South America is the bat species most specialized for piscivory. Using echolocation, *N. leporinus* captures small fish when they jump out of the water as well as by dragging its enlarged, clawed feet just below the surface in areas where surface disturbance has been detected (Schnitzler et al. 1994). The tail membrane between its legs further assists in transferring prey to the mouth. A few other bat species, including the fish-eating bat *Myotis vivesi* (Vespertilionidae) also consume fish. Piscivorous bats have distinct cranial shapes that enable high bite force at narrow gapes, necessary for processing fish prey (Santana and Cheung 2016). Aerial adults of aquatic insects can be important diet constituents for insectivorous bats. Although it consumed a broad diet of invertebrate species, the little brown bat *Myotis lucifugus* relied heavily on the mass-emerging mayfly genus *Caenis*, shown by molecular analysis of bat fecal pellets collected under roosts in southwestern Ontario, Canada (Clare et al. 2011).

Finally, it is worth noting that the hunting tactics of different vertebrate predators largely determine the size range of prey captured and the habitat, especially water depth range, where prey are encountered. Wading birds typically fish in water no deeper than 20–30 cm. Leg length and striking distance limit their success at greater depths. Diving and skimming predators such as kingfishers, osprey, and bats usually fish very close to the surface. Swimming predators typically feed at greater depth, either to minimize their own risk of predation or, especially if they are of large body size, to have more room to maneuver. The need to capture and swallow prey generally results in a rough correspondence between prey size and predator size, even in species able to extend their gapes or rend prey into pieces. The combination of a predator's depth range and size range may significantly affect the size and depth distribution of fishes in streams, and perhaps affect other members of the biota as well. Indeed, many vertebrate predators may have their impact on riverine communities by influencing the foraging location of their prey. As we shall see in subsequent chapters, the consequences can ramify widely through the food web.

9.4 Summary

Invertebrate and vertebrate animals in riverine food webs occupy a variety of trophic roles as consumers of algae, higher plants, non-living organic matter, and other animals. Their resources include those produced within the river and its floodplain, and external inputs derived mainly from the riparian zone. Microorganisms are important mediators of resource quality, especially the fungi that colonize leaf litter and biofilms of bacteria and other organisms that coat most wetted surfaces. Trophic organization in river ecosystems can be complex and indistinct, as many consumers are generalist feeders and often overlap broadly in their diets. Nonetheless, the classification of consumers into trophic categories provides useful insight into the variety of consumer roles and range of resources available. Initially, trophic categories were based primarily on the resource consumed, hence common categories included invertivore, herbivore, piscivore, and so on. Because so many consumers in riverine food webs are flexible feeders, it may seem that most are simply omnivores. However, trophic categorization can be made more robust by also specifying where the food is obtained (e.g., from the benthos or the water column) and morphological adaptations for capture and digestion.

Invertebrates typically are divided into functional feeding groups (FFGs) on the basis of resource category, where or how the resource is obtained, and morphological adaptations for food capture. Scrapers consume non-filamentous attached algae from substrates. Detrital shredders primarily feed on leaves and other products of terrestrial plants that fall into the stream and are colonized by microbes. Gathering collectors feed on fine particulate organic matter from depositional areas or crevices. Filtering collectors capture FPOM in suspension in streams using morphological structures or silk capture nets. Herbivore piercers are adapted to pierce individual filamentous algal cells and suck out the cell contents. Predators are adapted to catch and consume live prey by engulfing the prey or piercing and extracting the prey hemolymph. It should be noted that members of different invertebrate functional groups may consume the same resource: for example, fine particulate organic matter can be captured from the water column or collected from depositional locales. The main difference is not the resource, but the organism's method of acquiring it.

The FFG system assumes a direct correspondence between FFG composition and basal resources available at a stream location; thus, the use of FFGs to characterize the macroinvertebrate assemblage at a stream location provides insight into functional roles, basal resource availability, and the importance of allochthony vs autochthony. Studies that examine changing basal resource availability longitudinally in a river system or between shaded and open-canopy locations generally, but not invariably, find that FFG composition varies accordingly. Anthropogenic change can shift FFG relative composition, often in response to altered land use. Recent studies employing stable isotope and fatty acid analyses provide new insights into consumer diet, often showing that members of a particular FFG are consuming and assimilating energy from foods not usually attributed to them. Results generally reveal more flexibility in feeding and a greater degree of omnivory than expected.

Stream fishes consume virtually every resource available, and many individual species consume a wide range of resources, often changing diet over ontogeny and across environmental setting. Fish trophic categories rely primarily on what resources are consumed, but also may consider feeding location and morphology. There does not appear to be a single, generally accepted set of trophic categories, but the following are commonly used: herbivores, detritivores, planktivores, omnivores, benthic invertivores, midwater-surface feeders (largely on insects), and piscivores. Where appropriate, one can add specialized categories such as snail-eaters, scale and fin eaters, fruit-eaters, parasites such as lampreys, and so on. In the majority of stream settings, it usually is the case that invertivores comprise over half of the species list, except in large rivers, per cent herbivores increases downstream, and detritivores are uncommon.

From headwaters to river mouth, fish diversity generally increases, and trophic diversity does as well. Unquestionably, one finds a wider range of trophic categories in tropical than temperate streams, including more species of herbivores and detritivores, and more unusual specialists. This is especially apparent in large tropical rivers with extensive lateral floodplains where lake and backwater habitats connect to the river during high water. Plant production and detritus of both autochthonous and allochthonous origin are of great importance in these systems; consequently there is a greater role for mud and detritus feeding (which often supports the greatest biomass of fish), and for predation (which often dominates species richness).

Various aspects of fish morphology are useful in understanding habitat and feeding preferences of fishes. Variation in body size, mouth gape and position, dentition, and gut length are frequently found to be strongly associated with feeding role, as well as visual and chemosensory adaptations. The study of ecomorphology is based on correspondence between the trophic role of a species of fish and its morphological adaptations for capture and digestion. Persuasive examples include similarities in body form and jaw structure among unrelated piscivores, the greater gut length of herbivores and detritivores compared with invertivores and piscivores, and so on. Ecomorphological analysis also has its limitations, especially due to relatedness, as closely related species may have similar morphology and diet due to common ancestry.

Trophic categorization of fishes has its uses and its limitations. Different feeding roles can be identified within an assemblage of fishes based on differences in diet, feeding behavior, and morphology. What is also evident, however, is that across life stages, habitats, and seasons, many species are flexible in their diet, benefiting from their ability to exploit different food items based on changing availability of resources. Thus, studies often refer to the high frequency of dietary plasticity, or characterize many of the species present as omnivorous, generalists, or opportunists. Even in the tropics, where some wonderful examples of ecological specialization can be found, many observers have opined that a generalist or opportunistic feeding strategy seems to characterize the majority of species.

Although fishes are the principal vertebrate component of most riverine food webs, all vertebrate classes have representatives in running waters. In small headwater streams, salamanders and snakes may be important top predators; there are many species of fish-eating birds, and some that consume aquatic invertebrates; a few mammals feed primarily or exclusively on aquatic prey, and a surprising diversity of mammals do so at least occasionally. Other animals frequently are the main prey, but algal, higher plant, and detrital resources are consumed as well. Especially in larger rivers, the littoral zone and floodplain habitats provide feeding opportunities across all trophic levels for vertebrate consumers.

Larval amphibians in the temperate zone are found primarily in standing waters, but they can be diverse and abundant in tropical streams. The majority rasp algae and detritus from substrates and so are herbivores and detritivores, although unknown amounts of microbes and micro-organisms likely are ingested as well. Snakes and members of the Crocodilia are predators of fish and invertebrates in aquatic environments, but often consume other vertebrates. Diet studies indicate that aquatic snakes are generalist predators, consuming a wide range of fishes, amphibians, and other prey. Turtles are for the most part omnivores of sluggish streams and rivers, consuming substantial amounts of invertebrate and fish prey, but some are more specialized as herbivores or carnivores. Many orders of birds make use of rivers and streams as feeding habitat. Many are fish predators but some feed directly on invertebrates. Piscivorous birds capture fish and invertebrates by a wide variety of feeding modes, including underwater pursuers, waders, aerial plunge-divers, and aerial insectivores. Mammals ranging from shrews to raccoons to bears occasionally or frequently consume invertebrates and fish, while muskrats, beaver, and the South American capybara consume aquatic and riparian vegetation. Vertebrate predators have evolved a variety of hunting tactics that largely determine the size range of prey captured and the habitat, especially water depth range, where prey are encountered. The combination of a predator's depth range and size range may significantly affect the size and depth distribution of fishes in streams, and many vertebrate predators may have their greatest impact on riverine communities by influencing the foraging location of their prey.

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