Species Interactions

10

The assemblage of species within a stream reach forms a network of linkages and interactions that vary in strength and the number of species affected. The basal resources of algae and detritus, together with associated microorganisms and external energy subsidies, sustain higher consumers including herbivores, predators, the omnivores that blur trophic classification, and the pathogens and parasites that affect all. The availability of resources can limit the abundance of consumers (called bottom-up control), and consumers can regulate the abundance of their prey at lower trophic levels (called top-down control). Species often compete for the same limiting resources such as food or space, and successful competitors are able to retain their place in the assemblage while less aggressive or efficient species may be excluded. The interactions between grazers and algae, predators and their animal prey, parasites and their hosts, and competing species with one another constitute the primary linkages that collectively bind species together within food webs. In this chapter we focus on the ecological consequences and complexity of such linkages, and in the following chapter we explore the forces that ultimately determine which species are found together and the multiple food web interactions that structure lotic communities.

10.1 Herbivory

Primary producers, including algae, cyanobacteria, bryophytes, and vascular plants, are important basal resources in lotic food webs. Macrophytes also can be consumed directly by terrestrial and aquatic organisms, although much macrophyte production is consumed after entering the detrital pool, and phytoplankton play a relatively minor role in most free-flowing rivers. Grazing on benthic algae by invertebrates, some fishes, and a few amphibian larvae is the most important pathway of herbivory in streams, and has received by far the most study. Benthic algae vary in their distribution, growth form, and nutritional value, and grazers differ in their means of scraping and browsing this food supply. Thus, the species of algae that are consumed reflect their vulnerability to particular grazers, and possibly aspects of grazer preference as well. Grazers can have a number of impacts on algae, reducing their abundance, altering assemblage composition, and even stimulating algal growth and overall productivity through the removal of senescent cells and the recycling of nutrients.

10.1.1 Direct Interactions Between Consumers and Producers

The interaction between primary consumers and their food, of which benthic algae are of primary importance, is strongly dependent upon feeding modality of the consumer species, and traits, including growth form and chemical constituents, of the producer species (Steinman 1996; Holomuzki et al. 2013). Benthic algae are comprised of various algal groups and cyanobacteria, ranging in size from small individual cells to large filaments and colonies (Fig. 6.1), and intermixed with other surface-layer organisms including heterotrophic bacteria and micro-consumers such as protists and meiofauna, as well as organic material and extracellular compounds. Consumers of this mixture, often referred to interchangeably as benthic algae, periphyton, or epilithon, are many species of invertebrates, amphibian larvae, and fishes, categorized as grazers or herbivores.

As described in Chap. 9, some herbivores are able to scrape periphyton from hard surfaces, including snails with their rasping radulae, glossosomatid caddisflies with their mandibles, and some fishes such as the stoneroller *Campostoma* and loricariid catfish with sucker-like mouthparts that can remove all but the most tightly adherent and crevice-dwelling algae. Various mayflies, including in the Heptageniidae and Leptophlebiidae, can better be described as browsers and gatherers of upright forms of the algal

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overstory. As herbivorous species exhibit a range of feeding modalities, so also do algal species vary in size and growth forms that affects their vulnerability. Stalked, erect, and filamentous growth forms often are vulnerable to most herbivores, although filamentous algae can become too large for some. Prostrate forms often are vulnerable only to raspers and scrapers, and species of these feeding modes can have especially strong effects on most periphyton biomass and assemblages. Invertebrates are the dominant grazers in temperate latitudes, but freshwater fishes and amphibian larvae are important in some locations. Algae and organic matter are major dietary components for tropical fishes, which have been shown to strongly reduce attached algal biomass (Power 1984a; Flecker et al. 2002).

10.1.1.1 Grazer Impacts on Periphyton Assemblages

The impact of grazers on periphyton have been studied in both lab and field settings with a wide variety of innovative apparatus and experimental designs. In-depth reviews (Feminella and Hawkins 1995; Steinman 1996; Liess and Hillebrand 2004 , Liess and Kahlert 2007) agree that grazers exert strong control over periphyton biomass. Where herbivorous fish are plentiful, they have been found to wield considerable control over benthic primary producers. Exclusion of the stoneroller minnow *Campostoma* (due to the presence of a piscivorous fish) resulted in growth of filamentous algae, whereas introduced *Campostoma* caused rapid declines in algal biomass (Power and Matthews 1983). Tropical streams often contain numerous species of grazing fish, as well as algivorous insects, mollusks, crustaceans, and larval amphibians. Armored catfish (Loricariidae), popular for their diligence in cleaning algae from the walls of aquaria, have reached high abundances in southern Mexico, outside their native range. Exclusion experiments by Capps and Flecker (2015) documented very substantial decreases in algal biomass in the presence of grazing catfish, compared to where they were excluded (Fig. 10.1).

Snails and caddisfly larvae have proven to be highly effective grazers of periphyton in a number of studies, and share the traits of being individually large, relatively slow-moving, and well equipped with scraping mandibles or a radula. Periphyton biomass increased some five- to 20-fold relative to control substrates when the caddis larva *Helicopsyche* was excluded using tiles raised above the bed of a California stream (Lamberti and Resh 1983). Barriers of petroleum jelly effectively excluded another caddis larva, *Glossosoma*, from stone surfaces in a Montana stream, resulting in a fivefold increase in algal cell counts (McAuliffe 1984a). Lamberti et al. (1987) compared the mayfly

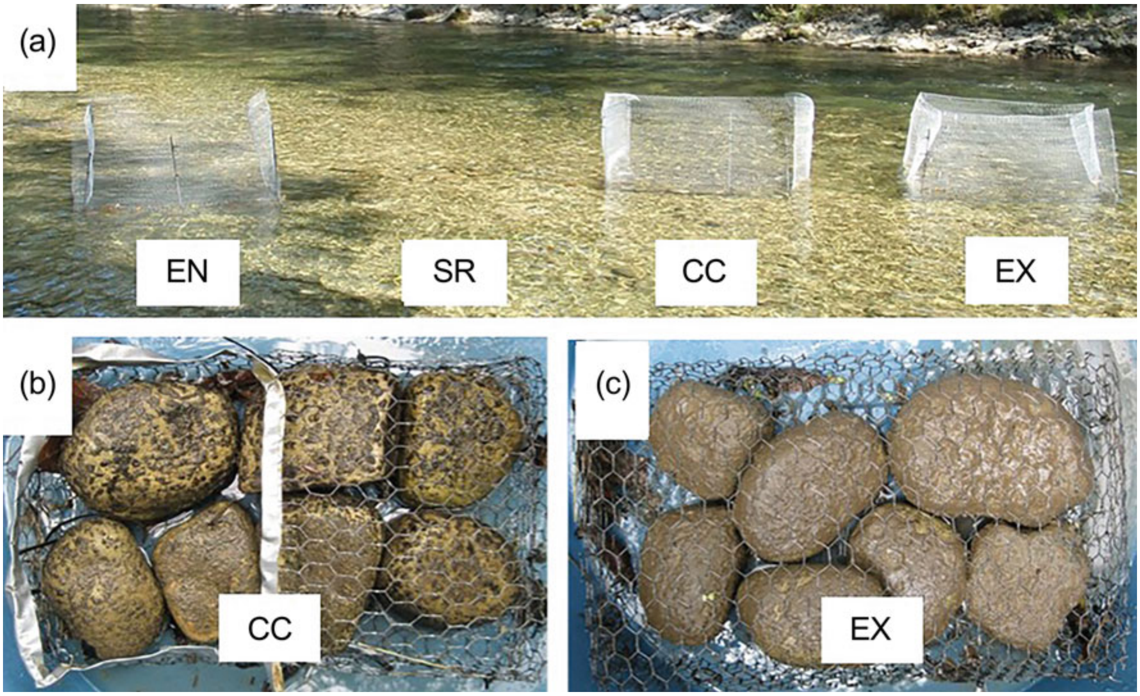

Fig. 10.1 A field experiment using cages to study the grazing impact of the armored catfish *Pterygoplichthys* (Siluriformes:Loricariidae) in a stream in southern Mexico. (**a**) An experiment with large cages (1.5 × 1.5 × 1.0 m length × width × height, constructed of poultry wire ~2.5-cm diameter). From left to right: *Pterygoplichthys* enclosure (EN), stream reference (SR), cage control (CC), and *Pterygoplichthys* exclosure (EX). (**b**) a cage control treatment from a small cage experiment (24 × 48 × 10 cm). (**c**) a small cage exclosure (Reproduced from Capps and Flecker 2015)

Centroptilum elsa, the caddis *Dicosmoecus gilvipes*, and the snail *Juga silicula*, which they characterized as a browser, scraper, and rasper, respectively. Laboratory streams were inoculated with algal scrapings, consumers were added at approximately natural densities nine days later, and development of the periphyton mat was monitored for 48 days. The effect of the mayfly was slight and confined to small (<2 cm diameter) patches, but *Juga* had a substantial impact and *Dicosmoecus* even more so. However, other studies have found grazing mayflies able to limit benthic algae. An experiment that enclosed the mayfly *Ameletus* at realistic densities in Plexiglas chambers containing natural stream bed material resulted in marked reductions in periphyton standing crops, even at densities of 0.5x ambient (Hill and Knight 1987) (Fig. 10.2).

As one might expect, suppression of grazers results in greater algal biomass, and suppression of periphyton results in fewer grazers. When all herbivorous invertebrates in a 50-m^2 reach of a Colorado mountain stream were reduced by daily electroshocking with a portable apparatus typically used to collect fish, algal biomass increased substantially in comparison to a reference stream (Taylor et al. 2002). Algal biomass can differ markedly at small spatial scale when the presence of predators restricts the local distribution of grazers. Rings of attached filamentous green algae developed along the margins of a Panama stream where wading birds effectively excluded grazing catfish, while algal biomass was much reduced in deeper water where catfish were safe to feed (Power 1984b). At the larger spatial scale of stream sections or entire streams, the abundance and growth of grazers varies with their food supply. In a small stream draining an area that had recently been clearcut, production of the mayfly *Baetis* was roughly 18 times higher than at a reference site (Wallace and Gurtz 1986). Mayfly guts contained mainly diatoms, and estimates of gut fullness from the open canopy stream were up to double those from the forested stream. Although algal cell densities varied little among sites, periphyton production (based on *Baetis* production and projected food consumption) was estimated to be nearly 30 times greater at the open site. Subsequent forest regrowth resulted in canopy closure, and after six years *Baetis* was much rarer and periphyton production had dropped tenfold. Because clearcutting affected the entire stream, recruitment rather than redistribution is the presumed mechanism.

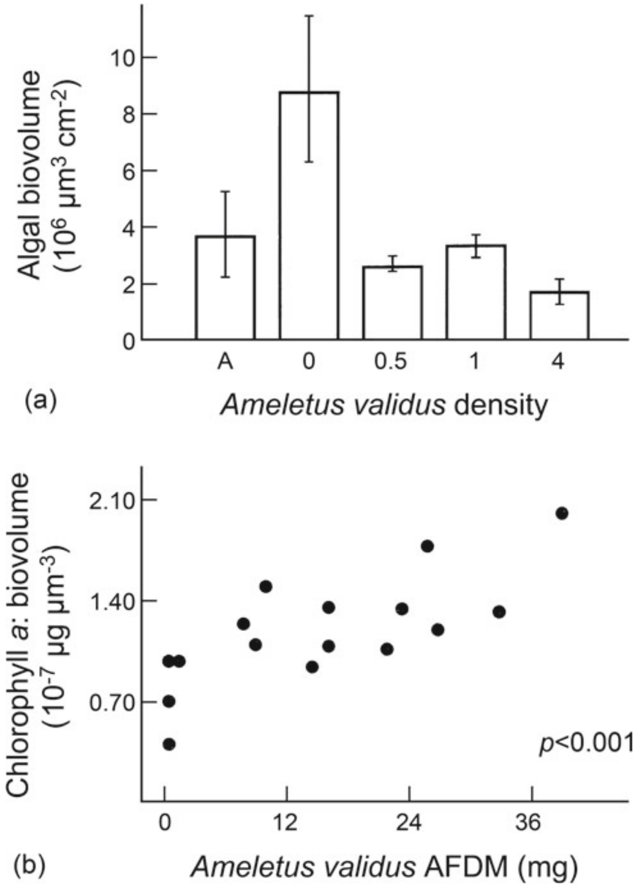

Fig. 10.2 The effect of density of the mayfly *Ameletus* on periphyton standing crop and quality. (**a**) Periphyton abundance under various grazing conditions. A: ambient densities on streambed; 0: cages with zero density; 0.5, 1 and 4: cages with 0.5x, 1x and 4x natural densities, respectively. Results were similar for chlorophyll *a* and AFDW. Note that even low densities of grazers reduced algal biovolume. (**b**) The ratio of chlorophyll *a* per unit biovolume increased significantly with *Ameletus* biomass (Reproduced from Hill and Knight 1987)

In a meta-analysis of 865 experimental studies reported in 178 publications, Hillebrand (2009) evaluated grazer control of periphyton biomass in all kinds of aquatic habitats to explore how environmental variables affected the degree of grazer control, and whether experimental results depended on aspects of experimental design. Overall, grazers removed an average of 59% of periphyton biomass, evidence that periphyton is indeed strongly controlled by herbivory. Different consumer groups had significantly different impacts. Two crustacean groups (isopods and amphipods) and trichopteran larvae had strongest effects, and dipterans (mainly Chironomidae) the weakest. The size of the grazer effect, which measured the proportional removal of periphyton, was positively associated with increasing algal biomass, temperature, and scarce resource availability. In lotic experiments in particular, laboratory experiments exhibited stronger effects than field studies, and within field studies, enclosures yielded significantly stronger grazing effects than exclosures. This is best explained by the fact that lab experiments confine grazers and their food without allowing consumer emigration, as do field enclosure experiments. In addition, lab experiments usually were stocked with higher grazer biomass and ran at higher temperatures. Length of experiment also appears to influence outcome, as grazing effects become more pronounced over time, especially when spatially confined. This highlights the challenge of reproducing realistic lotic environments in lab settings compared to field experiments.

Species and trait composition usually change in response to grazing, which tends to reduce species richness as well as dominance by a few species, thereby increasing the evenness of species representation in the assemblage (Hillebrand 2009). Upright, overstory, and loosely attached algal taxa are vulnerable to a wide range of grazers, whose presence often shifts benthic assemblages toward prostrate, understory forms. In mesocosm experiments using various combinations of grazing by a snail, a mayfly, and a caddisfly, several prostrate diatom species were dominant on grazed clay tiles, erect growth forms were more abundant in ungrazed controls and in snail alone treatments, and two species of green filamentous algae and a colonial species of cyanobacteria were present only in ungrazed controls (Holomuzki and Biggs 2006). A shift towards basal cells of the grazer-resistant chlorophyte *Stigeoclonium* occurred in response to grazing fishes in a stream in the Andean foothills of Venezuela (Flecker et al. 2002) and to snails in flow-through channels within a stream in Tennessee, US (Rosemond et al. 2000).

The components of the periphyton mat that are most affected by herbivory can vary with the species of grazer and with their feeding mode. Grazing by a snail (*Juga*) and a caddisfly larva (*Dicosmoesus*) caused broadly similar changes to benthic algal assemblages, reducing algal assemblages to representation mainly by the adnate diatom *Achnanthes* and basal cells of the filamentous green alga *Stigeoclonium* (Lamberti et al. 1987). However, it also is possible for two herbivores to have quite different effects, as Hill and Knight (1987, 1988) demonstrated in their comparison of the caddis *Neophylax* and the mayfly *Ameletus*. Loose and adnate layers were sampled separately and *Ameletus* affected principally the former, causing declines in motile diatoms including *Surirella spiralis* and several species of *Nitzschia*. *Neophylax* affected both layers but its major impact was through reducing the abundance of a particularly large, adnate diatom that comprised the bulk of total periphyton biovolume.

Environmental conditions have a strong influence on algal growth form, which in turn affects what herbivore feeding modes are likely to most effective (Fig. 10.3, Vadeboncoeur and Power 2017). Where the scouring effect of storms and grazing pressures are strong, one finds thin films <0.1 mm thick of small, tightly appressed or motile diatoms. In high light and low nutrient environments, tightly attached felts 0.1–2 mm thick of nitrogen-fixing cyanobacteria usually develop, with diatom overgrowth, providing forage for algivorous fishes. When grazing pressure is low or floods are few, mats of filamentous chlorophytes such as *Stigeoclonium* and *Cladophora* develop, usually with an epiphytic layer of diatoms. The first two assemblage types persist under intense grazing, whereas the third occurs when green algae have escaped grazing for sufficient time to become too large and unwieldy for most consumers (but epiphytic diatoms growing on macroalgal filaments may be heavily grazed by small invertebrates).

10.1.1.2 Food Quantity and Quality

The high efficiency of grazers at reducing biomass of benthic algae has several possible explanations (Hillebrand 2009). Microalgae are high-quality food in terms of P and N content. Grazers are large relative to their food items, and rasping or scraping periphyton from hard substrate surfaces allows high proportional removal of periphyton biomass, with different taxa of grazers preferentially using different layers of the periphyton (Steinman 1996). As reviewed above, grazers consume substantial quantities of benthic algae, which supports substantial grazer biomass and in turn contributes to higher trophic levels. However, food quantity alone, commonly measured as biomass or chlorophyll a, likely is an insufficient measure of the consumer's resource base. Food quality, assessed from nutrient and fatty acid content of the resource, and assimilation and growth efficiencies of the consumer, provides important insights into the resource basis of grazers and energy transfers to upper trophic levels.

A grazer's food supply may be limiting because nutrient needs of the consumer are not met by the relative availability of nutrients in the producer, which instead is more likely to reflect their relative availability in the environment (Sterner and Elser 2002). Ecological stoichiometry theory predicts that the relative imbalance between particulate nutrients in consumer and producer biomass determines nutrient limitation of consumer growth, and also the rates at which consumers recycle nutrients. The stoichiometry, or the ratio of elements, of food resources is an important indicator of food quality as it affects the growth and reproduction of primary consumers. High food quality corresponds to low periphyton carbon (C) content relative to other nutrients, such as nitrogen (N) and phosphorus (P).

Research shows that primary producers generally have high and more variable carbon to nutrient ratios relative to aquatic consumers. Incubating periphyton in once-through streamside flumes provided with different stream water concentrations and N:P ratios, Stelzer and Lamberti (2001) found that the N and P content and N:P ratios of periphyton tracked stream water concentrations. Further, growth of the snail *Elimia livescens* was greater on a diet of periphyton grown at higher streamwater P concentrations, but only when food was limited in quantity, suggesting that streamwater dissolved P influenced *Elimia* growth through its influence on periphyton chemical composition (Stelzer and Lamberti 2002). By manipulating nutrients, light, and

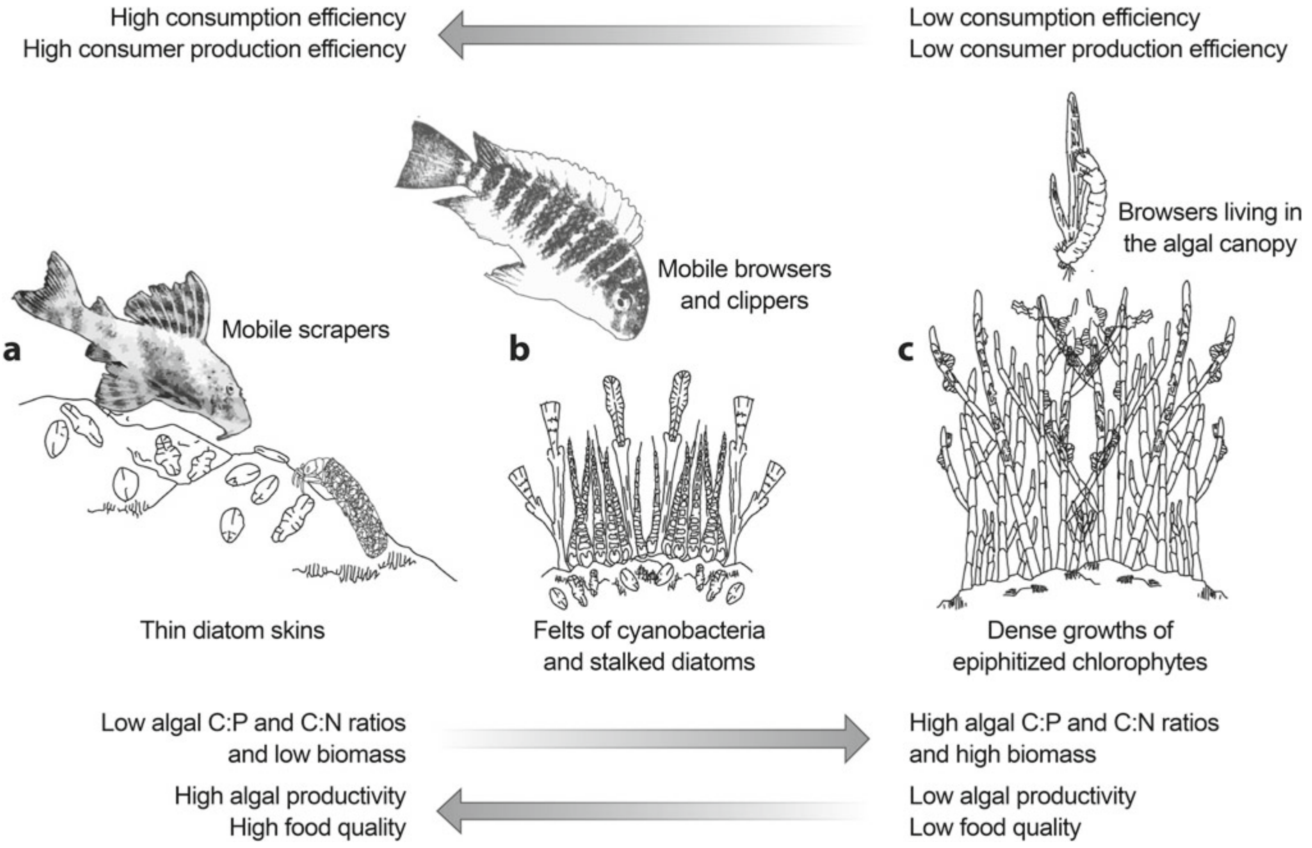

Fig. 10.3 Schematic of the grazer-benthic algae interaction between different grazing modes and algal growth forms. (**a**) Mobile grazers with scraping mouth parts can maintain barely perceptible, thin films of rapidly growing, nutritious diatoms. Although biomass is low, algal quality is high due to high concentrations of nitrogen and phosphorus relative to carbon (low C:N). (**b**) Cyanobacteria in the family Rivulariaceae and stalked diatoms persist in the presence of grazers that consume loose algae from the low-growing felts that coat rocks. (**c**) When grazing pressure is relaxed for periods of weeks, green algae such as *Cladophora* form dense mats that provide habitat for small grazers. As biomass accumulates, algal quality declines because there are high concentrations of carbon in the algae relative to nitrogen and phosphorus. Note: organisms are not to scale (Reproduced from Vadeboncoeur and Power 2017)

grazer abundance in flow-through channels in a Tennessee, US, stream, Rosemond et al. (2000) found that periphyton exhibited less P limitation and snails had higher growth rates when nutrient supply was elevated. And in a field survey of 41 southern New Zealand streams, Liess et al. (2012) reported that periphyton C:N correlated with variation in water column dissolved inorganic N; in addition, the abundance of grazers, and of invertebrates in general, was higher in streams with higher food quality as indicated by lower C:N ratios.

In contrast to the relatively high carbon to nutrient ratios of primary producers, aquatic consumers often have lower and more constant C: nutrient ratios, reflective of their greater need for N and P in their tissues and relatively homeostatic regulation of their body chemistry. Benthic macroinvertebrates collected from streams in the Midwestern US exhibited little variation in body C, N, and P concentrations and ratios within taxa, consistent with the view that many animals exhibit relative homeostasis in elemental composition (Evans-White and Lamberti 2005). However, elemental composition differed among taxonomic groups, as insects, mollusks (soft body tissue only), and crustaceans exhibited declining C:P and N:P ratios, in that order (Fig. 10.4). Interestingly, the range of N:P for benthic insects was greater than in other taxonomic groups for which data were available.

Because animals often have relatively constant tissue stoichiometry and lower C:nutrient ratios when compared to primary producers, food quality as reflected in its elemental composition is typically much more variable for herbivores than it is for fish and invertebrates that consume animal prey (Sterner and Elser 2002). Thus herbivores, and especially herbivorous fish with their boney skeletons, have greater potential for their growth and reproduction to be limited by nutrients rather than energy or other factors. Nutrient demand of the consumer relative to nutrient composition of its resource also has important consequences for nutrient excretion and recycling, discussed further in a later section.

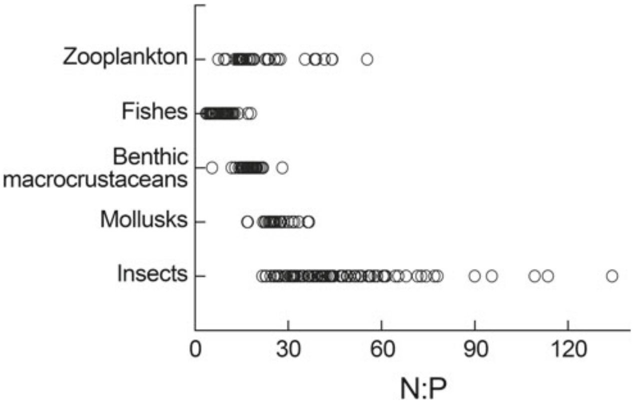

Fig. 10.4 Molar nitrogen to phosphorus ratios of different animal groups. Insect, mollusk, and benthic crustacean data are from streams in Indiana–Michigan and Wisconsin. Each point represents a taxon from a particular stream. Fish and zooplankton data from published sources (Reproduced from Evans-White and Lamberti 2005)

Environmental conditions can alter the stoichiometry and thus food quality of benthic algae to their consumers. The light∶nutrient hypothesis (LNH) posits that increased light intensity may increase algal C∶ nutrient ratios under nutrient-limited conditions because autotroph C-fixation rates increase in response to light (Sterner et al. 1997). As a consequence, herbivore growth rates are expected to be greatest at intermediate light-to-nutrient ratios, where high-quality food is expected to be most abundant. Herbivores are hypothesized to be C limited at low light-to-nutrient ratios and nutrient limited at high light-to-nutrient ratios. In support of this expectation, Fanta et al. (2010) found that periphyton P increased in laboratory and natural streams as water column P increased, and decreased as light increased. Using fast-growing juvenile snails (*Gyraulus chinensis*) in lab streams, Ohta et al. (2011) observed results consistent with the LNH. As light intensity increased, so did periphyton biomass as well as C:N and C:P ratios in periphyton tissue. Snail growth rate and the phosphorus content of its gonadal tissue were maximized at an intermediate light intensity and were most responsive to periphyton C:P ratios under the oligotrophic conditions of the experiment. The light-nutrient interaction occurs because light can only reduce periphyton nutrient content in oligotrophic environments (Fanta et al. 2010), and so the results of experimental studies are most likely to depend on the range of light levels and nutrient concentrations employed. Using three levels of light and two concentrations of P in large, flow-through experimental streams, Hill et al. (2011) found that periphyton C:P and C:N ratios increased with light augmentation and decreased with P enrichment, consistent with the LNH. Manipulation of light (open vs. shaded) and nutrients (N + P in a slow release mixture) in cobble-bed riffles of three headwater streams in southeastern Queensland, Australia, influenced grazer growth rates as revealed from head capsule widths at the beginning and end of the 42-day experiment (Guo et al. 2016a). Growth of the mayfly *Austrophlebioides* declined under higher levels of light and nutrients, while growth of the caddis larvae *Helicopsyche* responded positively to nutrient additions regardless of light intensity. High quality food was most abundant under low light intensity and nutrient-enriched conditions, and was primarily related to periphyton food quality in terms of its C:N content rather than algal food quantity measured as chlorophyll *a*.

Tests of the LNH in stream ecosystems are relatively few and, when examined collectively, provide mixed support for the LNH. Most likely, the variation in outcome is due to the wide variety of environmental contexts in which lab and field studies have been conducted. Important contextual factors that could influence experimental outcomes include but are not limited to consumer traits, including body size, tissue stoichiometry, and feeding mode; periphyton traits, including the species composition of algae and presence of detritus and microbes; and physicochemical factors, including stream nutrient composition (which influences benthic algal nutrient composition), flow velocity, depth, and ambient light.

Fatty acids, particularly long-chain polyunsaturated fatty acids (PUFA), are considered essential for animal diets. The higher PUFA content of algae relative to plant detritus is a key reason for their higher quality as food, and because invertebrates and fish have limited ability to synthesize fatty acids, their dietary acquisition is important to freshwater animals (Guo et al. 2016b). In an experimental test of the LNH hypothesis, described above (Hill et al. 2011), light also influenced the composition of fatty acids in periphyton, and effects were strongest in phosphorus-poor streams (Fig. 10.5). Experimental manipulation of light and nutrients in a subtropical stream in Queensland, Australia, altered the fatty acid composition of stream periphyton, which in turn influenced fatty acid content of stream herbivores (Guo et al. 2016c). The combined effects of shading and added nutrients led to increased levels of highly unsaturated fatty acids in periphyton, and increased similarity in fatty acid content between stream grazers (the mayfly *Austrophlebioides* and caddisfly *Helicopsyche*) and periphyton. Large instars of both grazers showed higher growth in response to these changes, indicating that the concentration of highly unsaturated fatty acids in periphyton is an indicator of periphyton food quality. There also is evidence that algal biofilms on the surfaces of leaf litter improve the nutritional quality of terrestrial inputs for invertebrate shredders (Guo et al. 2016d)). The stream invertebrate shredder (*Anisocentropus bicoloratus*, Trichoptera) reached larger sizes on leaves that developed an algal biofilm under enriched nutrient conditions, evidently by increasing leaf PUFA content.

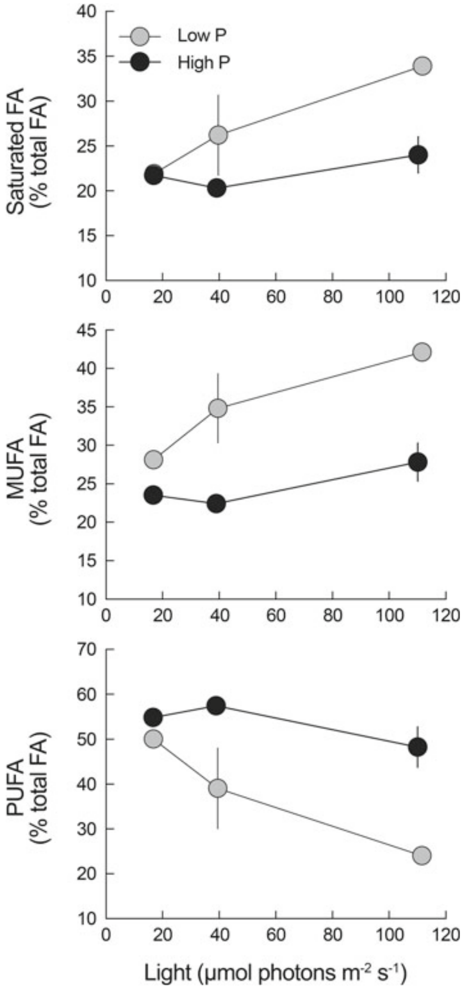

Fig. 10.5 Influence of three levels of light and two concentrations of phosphorus on the fatty acid content of periphyton in large flow through streams (22 m long by 0.3 m wide), supplied with unfiltered, low-phosphorus water from a nearby spring-fed stream. Symbols represent mean ±1 SE (n = 2). SAFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids (Reproduced from Hill et al. 2011)

10.1.1.3 Behavioral Responses

Algae are patchily distributed, from the smallest scale of the surface of an individual substrate, to an intermediate scale such as from stone to stone, through larger scales such as open versus canopied sections of streams. Although some herbivores might feed essentially at random, an ability to perceive and respond to this patchiness ought to be advantageous. Grazers can concentrate in food-rich locations through behavioral mechanisms at small and even relatively large scales, and such non-random foraging has been established in both vertebrate and invertebrate grazers of periphyton. Richards and Winshall (1988) studied grazer distribution at small scales in an alpine stream, using natural stones that were selected based on visual assessment of periphyton abundance and in some instances scraped to produce patches of various widths. Stones were replaced in the stream under glass viewing boxes, and insect presence then was determined by photography. Within one to two days, grazing mayflies of the genus *Baetis* were concentrated in patches rich in periphyton. In laboratory microcosms containing rocks with algae from a nearby stream, *Baetis* distributions were unselective when algal biomass was homogeneously distributed, but clustered on high-food rocks when it was heterogeneously distributed (Alvarez and Peckarsky 2005). Detailed analyses of foraging in the caddis larvae *Dicosmoecus* (Hart 1981) and the mayfly nymph *Baetis* (Kohler 1984) document that these insects spend much more time in periphyton-rich patches than would be expected under a model of random movement. When individual *Dicosmoecus* entered an area with abundant periphyton, gathering movements of the forelegs and the rate of mandibular scraping both increased. In addition, overall movement rate slowed, and individuals tended to turn back upon reaching a patch boundary. As a result, time spent in rich patches was two to three times what would be expected by chance alone.

The ability to perceive spatial heterogeneity in food supply and respond by simple movement rules that tend to concentrate foraging in regions of high reward is termed area-restricted search. When the periphyton attached to an artificial substrate were scraped to create a checkerboard design that covered only 20% of the substrate surface, *Baetis* spent up to 80% of its time in food patches (Kohler 1984). By comparing the area searched to the smallest area that circumscribed the sequence of movements, Kohler determined that these mayflies searched food-rich patches very thoroughly. Moreover, search behavior upon departure from a patch was influenced by patch quality. Search intensity was much greater just after departing a high quality patch, as evidenced by high thoroughness and low movement rates in comparison to movements following departure from patches of lower quality (Fig. 10.6).

Whenever highly mobile herbivores concentrate where algal resources are rich, crowding can reduce the rate of return for an individual grazer to approximately what it would experience in a less productive but less crowded region. A likely consequence is for the abundance and biomass of grazers to increase proportionately with algal productivity, but for foraging gain per individual to be roughly constant. Power (1983) observed just this pattern in the distribution of armored catfish among pools in a Panamanian stream. Shaded pools were less productive and supported a lower abundance and biomass of herbivorous fish compared to open pools. However, individual growth rates were similar across this resource gradient (Fig. 10.7). Movements of individuals among pools in a manner similar to the finer

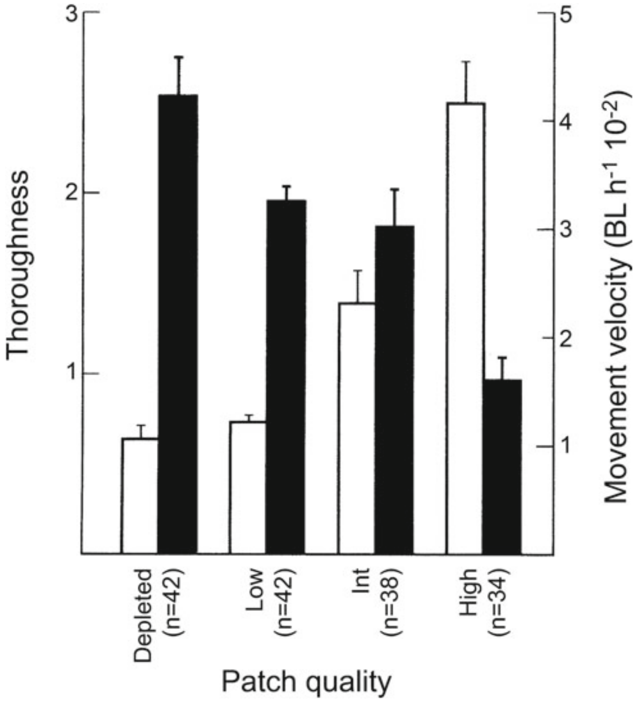

Fig. 10.6 The influence of patch quality (periphyton cell density) on *Baetis* search behavior immediately after leaving a patch. Thoroughness of searching (open bars) increases and movement rate (solid bars) decreases with increasing patch quality (Reproduced from Kohler 1984)

scale foraging behaviors of *Baetis* and *Dicosmoecus* presumably result in this pattern, referred to as the ideal-free distribution.

In sum, grazing animals respond to locations of high periphyton abundance, both by shifts in distribution and, if conditions persist for long enough, by population recruitment. These concentrations of grazers can either reduce or enhance variation in the distribution and abundance of periphyton, and as we shall see in the next section, influence the composition and physiognomic structure of the periphyton assemblage.

10.1.2 Indirect Effects of Grazer-Resource Interaction

Grazers affect the periphyton by direct consumption, by physical disruption of algal mats, and through indirect pathways, especially by nutrient regeneration. The previous section summarized direct effects of consumption, including reduction in periphyton biomass, compositional changes including a reduction in the overstory component, and marked differences in effects depending on the identity of the grazer. In addition to these direct effects, grazing can indirectly influence algal nutrient content, productivity, diversity and heterogeneity (Fig. 10.8). The meta-analysis by Liess and Hillebrand (2004) that found a strong, negative relationship between grazing and algal biomass, also revealed that on average, grazing altered algal nutrient ratios, produced algae with relatively higher P concentrations, reduced the area-specific productivity of algae but enhanced algal productivity per unit biomass, increased the spatial heterogeneity of algae, and reduced algal diversity. In general, these effects were significant but of lesser magnitude than direct consumption, and effect sizes correlated with the magnitude of biomass reduction.

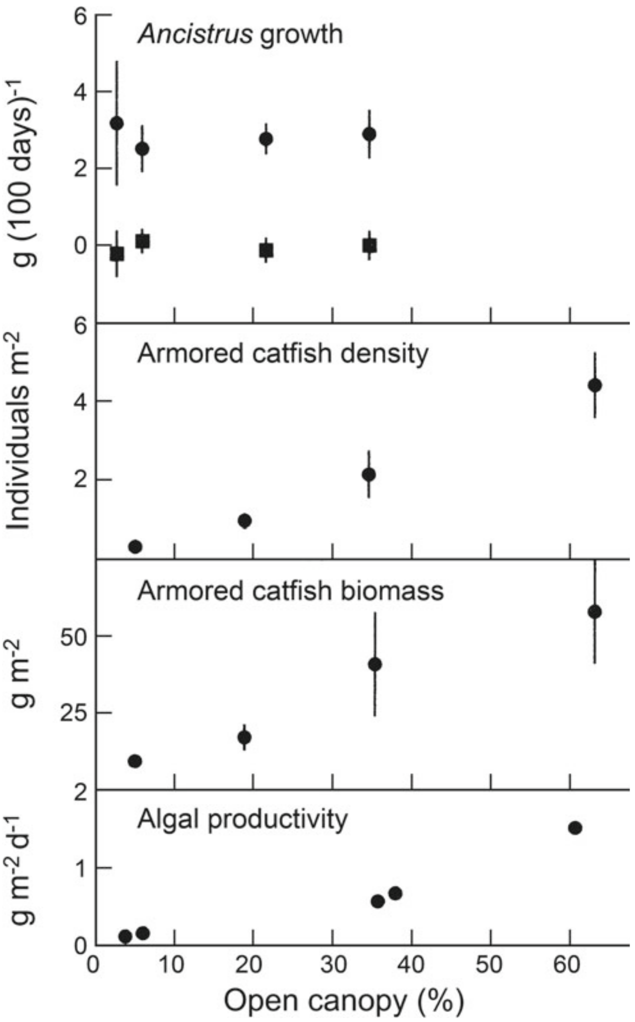

Fig. 10.7 Evidence that the loricariid catfish *Ancistrus* conforms to an ideal-free distribution. Algal productivity increases in relation to openness of canopy. Density and biomass of catfish increase proportionately with algal productivity, but growth rate (●, rainy season; ■, dry season) is constant. Two standard errors are shown (Reproduced from Power 1983)

Several additional pathways can account for the diverse effects grazers can have on the quality, quantity, and productivity of periphyton (Fig. 10.9). First, periphyton grazing that dislodges or consumes substantial amounts of detritus is

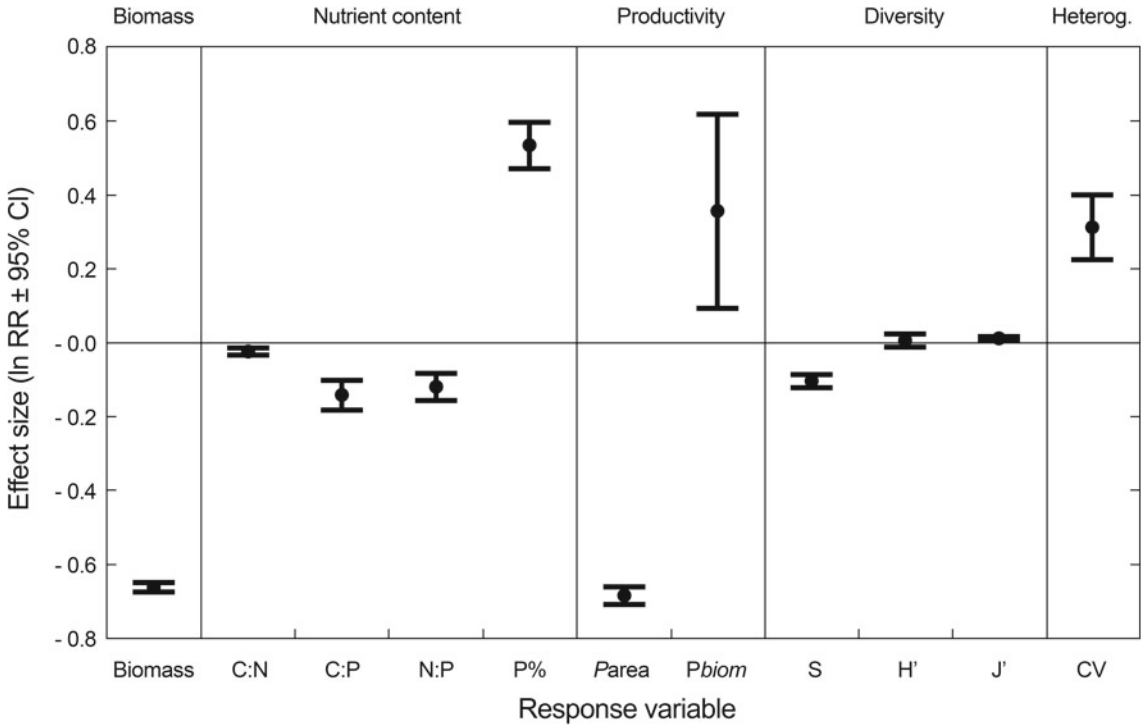

Fig. 10.8 The mean effect size of grazing based on a meta-analysis of 495 experiments reported in 116 studies, based on the log of the response ratio between grazer and control treatments. Periphyton response variables included biomass, nutrient content as percent phosphorus and molar ratios, area- and biomass-specific productivity, taxon diversity metrics and spatial heterogeneity estimated from measurement variance within grazer and control treatments. Diversity measures include number of taxa (S), Shannon diversity (H'), and relative evenness of abundance among taxa. Effect and sample size vary among response measures (Reproduced from Liess and Hillebrand 2004)

likely to result in lower C:N and C:P ratios of the remaining periphyton. Second, by reducing algal biomass, herbivores can indirectly reduce overall nutrient demand and increase nutrient uptake per unit biomass, thereby alleviating nutrient limitation of periphyton mats and increasing particulate nutrients in autotroph tissues. Increased diffusion to the periphyton layer and changes to species composition may also affect nutrient uptake rates. Third, grazer excretion and/or egestion of nutrients can directly increase the supply of nutrients available to the periphyton. Any of these effects can influence C:N:P ratios of the periphyton, and hence food quality for grazers.

Another meta-analysis by Hillebrand et al. (2008) focused on the ecological stoichiometry of grazer–periphyton studies found that grazers generally lowered C:P and C:N ratios, indicating that grazed periphyton had higher P and N content. Grazer effects on periphyton nutrient ratios varied with the nutrient content of grazers and their food, as well as grazer biomass, the amount of biomass removal, and water column nutrients. In addition, Hillebrand et al. (2008) found a trend towards increased periphyton particulate N relative to particulate P, such that periphyton N:P increased with grazer density.

Subsequent studies have more directly examined the importance of nutrient recycling due to consumer excretion and egestion by explicitly comparing elemental composition of grazer and resource. Ecological stoichiometry, or the study of the balance of elements in ecological processes, predicts that an herbivore with a high body particulate P and thus a low body N:P ratio would be more likely to experience P-limitation than would another herbivore with lower body P and a higher body N:P ratio (Sterner and Elser 2002). One would also expect that P-rich species would selectively retain P and excrete waste with a high N:P ratio. A study of nutrient excretion by snails (body N:P = 28) compared with crayfish (body N:P = 18) supports this prediction (Evans-White and Lamberti 2005). As expected from its body elemental ratio, crayfish excretion had a significantly higher ratio of ammonium: soluble reactive phosphorus than did snails that had higher body N:P ratio. Additionally, the N content of periphyton in lab streams was higher in the presence of crayfish than snails, and the P content was lower in the presence of either grazer, suggesting that benthic grazers can alter nutrient composition and limitation of periphyton via nutrient excretion.

Comparison of two grazers of a Neotropical stream that represent extremes of body stoichiometry in vertebrates provide further insights. Due to their extensive, P-rich bony-plated armor, the armored catfish *Ancistrus triradiatus*

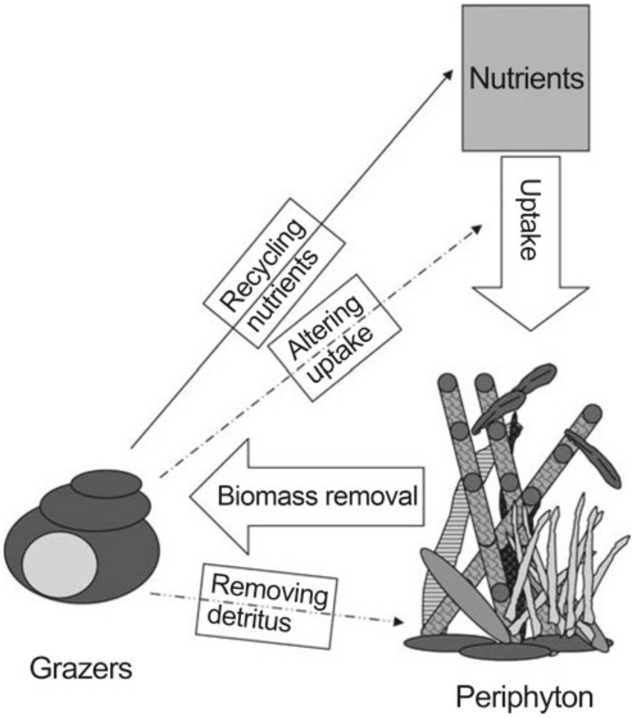

Fig. 10.9 Illustration of the most important direct and indirect effects of grazers on nutrient stoichiometry. Grazers can influence periphyton carbon to nitrogen to phosphorus ratios by removing detritus, which reduces the carbon content of periphyton; by reducing detritus and senescent cells by grazing and dislodgment, thereby increasing nutrient and light availability to actively growing cells; and by recycling nutrients via excretion and egestion (Reproduced from Hillebrand et al. 2008)

has a high body P, and thus low body N:P, whereas early tadpoles of the frog *Rana palmipes* have low body P and thus a high body N:P. As would be expected, catfish retain P and excrete at a high N:P ratio, and tadpoles do the opposite (Vanni et al. 2002). Using a grazer exclusion design in which periphyton was exposed to both grazing and excretion or protected from grazing but exposed to consumer excretion, Knoll et al. (2009) demonstrated that grazer identity can affect periphyton nutrient stoichiometry through both grazing and excretion. Water nutrient concentrations of soluble reactive phosphorus were highest in the tadpole treatment, while nitrate-N concentrations and N:P ratios were highest in the catfish treatment. Periphyton N:P increased in the presence of catfish and decreased in the presence of tadpoles, indicating that the elemental composition of grazers had an effect on periphyton N:P ratios mediated through grazer excretion and streamwater chemistry. Catfish stimulated the growth of periphyton protected from grazing but exposed to grazer excretion, but tadpoles did not, consistent with other evidence that periphyton in this Neotropical stream are primarily N limited.

As the above example indicates, consumer excretion is likely to be most influential when periphyton are limited by the preferentially excreted nutrient, and in oligotrophic systems when nutrients are in short supply. To test this prediction, Evans-White and Lamberti (2006) compared the effects of grazing by stoichiometrically disparate consumers—snails and crayfish—under ambient and elevated streamwater P concentrations. They observed a higher C:P and lower P concentrations in periphyton in the crayfish treatments, as expected from their lower body N:P. At elevated P, however, consumer identity no longer affected periphyton elemental composition, suggesting that consumer-driven nutrient dynamics and consumer identity are more likely to be important when nutrients are in short supply. Clearly, the elemental composition of streamwater, periphyton, and grazers together determine the importance of grazer excretion in alleviating stoichiometric constraints on producer growth. Where the mis-match between elemental composition of grazer and its food supply is substantial, consumer growth may be limited by food quality, and producers may be limited by the volume and stoichiometry of consumer excretion and egestion.

Grazers can also change the elemental composition and the nutrient demand of the periphyton community by shifting community composition toward grazer-resistant taxa that might differ in their C:N:P stoichiometry. This was shown in a multi-factorial lab experiment that assessed periphyton nutrient stoichiometry, algal taxonomy and biomass, and dissolved nutrients in response to grazing by the gastropod *Viviparus viviparus* (Liess and Kahlert 2007). Grazing resulted in strong dominance by the mucilage-producing algae *Chaetophora* and had a pronounced effect on periphyton nutrient stoichiometry because mucilage has high C and N content, but low P content.

10.1.3 Disturbance and Herbivory

The interaction between grazers and periphyton generally is considered to be strongest under stable environmental conditions and diminished when environmental conditions are extreme or highly variable, often referred to as the “harsh-benign” hypothesis. Most field studies of grazing have been conducted under low flow conditions, and thus do not adequately represent interactions during the more physically stressful conditions associated with environmental extremes that can occur seasonally or episodically (Feminella and Hawkins 1995). Such extremes are commonly referred to as disturbances. Often, disturbances are generated by abiotic factors, such as changes in flow or temperature; however, they can also be generated by biotic agents such as invasive species. Many of the best documented examples of disturbance influencing herbivory involve extremes of current.

Grazing may result in an algal assemblage that is less vulnerable to scouring by floods, presumably by reducing mat build-up. When the periphyton in laboratory streams subjected to variation in grazing pressure by the snail *Elimia clavaeformis* experienced a common scour disturbance, the structural characteristics of the periphyton exposed to snail grazing were more resistant to change than periphyton communities with no previous exposure to snails (Mulholland et al. 1991). Because stream current influences the architecture and taxonomic composition of periphyton, it creates conditions under which some species can forage more effectively than others, and facilitates conditions whereby interactions between a given species and flow can influence populations of other grazing species. For example, in a mesocosm experiment with *Glossosoma verdona* (Trichoptera) and *Drunella grandis* (Ephemeroptera) (Wellnitz and Poff 2012), senescent filaments of *Ulothrix* (a green alga) became abundant under low flow conditions, entangling *Glossosoma* and causing weight loss and mortality. However, *Drunella* was able to reduce senescent filaments across all experimental treatments, and *Glossosoma* survivorship and weight gain in slow current was positively correlated with *Drunella* density.

Experimental reduction of grazers at locations of differing current velocity revealed an interaction between grazing and current in a Colorado stream (Opsahl et al. 2003). After 45 days, tiles that were experimentally electrified to reduce grazer populations had significantly fewer grazers and more than twice the algal biomass compared with control tiles. Greater algal abundance on control tiles in slow currents suggested that grazers differed in their ability to regulate algae across the current velocity gradient. Hintz and Wellnitz (2013) observed a subsidy-stress effect of increasing current velocity on accumulation of algal biomass in artificial streams, as increasing current first facilitated biomass accumulation (subsidy) but at higher velocities removed it (stress). Determinants of either the facilitation or reduction of biomass varied with the identity of three grazing mayflies, presumably the result of differences in tolerance of species to variations in current. Algal biomass and assemblage composition showed some variation between wet and dry seasons in Hong Kong streams that was attributable to spate-induced disturbance caused by monsoonal rains during the wet season (Yang et al. 2009). Averaged across four streams, algal biomass was only modestly greater in the dry season, possibly due to strong grazing by the algivorous fish *Pseudogastromyzon myersi*.

In summary, grazing by invertebrates, amphibian larvae, and fishes is an important energy pathway to higher trophic levels. Grazing has strong direct effects on the abundance, physiognomy, and species composition of benthic algae, and can influence algal nutrient availability and productivity. In this chapter we have limited our focus to the interaction between just these two trophic levels. However, benthic algae are influenced by a number of different environmental variables (Chap. 6), grazers may be as influenced by their predators as their food supply (Sect. 10.2), and these two-way interactions are embedded in a much more complex food web with interactions across multiple trophic levels (Chap. 12). As we broaden our perspective to include all of the environmental variables that affect periphyton, including seasonal and episodic disturbance as well as the predators and parasites that can regulate grazer abundance, it becomes increasingly apparent that biological assemblages are complex entities subject to multiple, interacting controls.

10.2 Predation

Predation is ubiquitous. All heterotrophic organisms are prey for others at some stage of their life cycles, and many species encounter predation risk throughout their lives. The potential effects of predation are diverse, and include reduction in abundance or even the elimination of a species from a region, restrictions on behavior, habitat use, and foraging efficiency that affect growth rates and reduce fitness, and adaptation via natural selection to persistent predation risk. Top predators can cause a potential cascade of interactions through the food web, directly affecting prey by reducing their abundance and changing their foraging behavior, and indirectly influencing additional species to which the prey are linked as food or competitors. Furthermore, changes in energy pathways and species composition may have consequences for nutrient utilization and regeneration. In this chapter we consider the predator-prey linkage as an interaction that has effects on populations, directly through consumption and mortality, and indirectly through behavioral and morphological adaptations that may entail some fitness cost to the prey in order to survive. In Chap. 12 we will examine how predation can trigger trophic cascades that have consequences for the entire ecosystem.

10.2.1 The Predator-Prey Interaction

All predators show some degree of preference, feeding mainly on certain species, size classes, or types of prey. A large literature documents the diet of vertebrate and invertebrate predators in running waters. It is evident that predation is complex and its influence depends in part on aspects of the predators, including their morphology, foraging mode, means of prey detection, and size relative to the size of prey. Prey characteristics also play a major role in predation, as prey abundance, activity, visibility, and size strongly influence detection probability, attack, and capture rates. Predator and prey behavior and population size can vary seasonally and across habitats, adding spatial and temporal complexity in predator-prey interactions. Further, most predators must also contend with their own predation risk from larger predators and from aggressive competitors.

10.2.1.1 Prey Selection by Fishes

Most fishes of temperate steams, including the younger life stages of more piscivorous fish, feed on invertebrates. Aquatic invertebrate prey can be captured from the benthos and as individuals suspended in the water column, referred to as "drift". Terrestrial invertebrates falling onto the water surface also can be an important diet supplement for aquatic predators. By comparing prey abundance, average size, and species composition collected in fish stomach contents with the characteristics of the aquatic invertebrates collected in stream habitats, numerous studies have found prey abundance and size to be strong predictors of fish diet. In general, the number of prey eaten increases with prey abundance for all types of predators, at a decelerating rate due to the time limitation imposed by the handling and ingestion of individual food items. This relationship is known as a functional response curve. Whenever more than one type of prey is present, gut analyses generally find that prey that are abundant in the environment are also common in the diet (Allan 1981). However, the correspondence often is not 1:1, indicating some degree of predator selectivity. Prey choice can be strongly influenced by contrast, motion, and size, all of which serve to make certain prey more conspicuous. Larger prey items are expected to be preferred both because they offer a greater energy reward and because they are more readily detected.

Feeding trials using juvenile coho salmon *Oncorhynchus kisutch* in lab streams nicely illustrate the variables influencing fish reaction to prey floating on the water surface (Dunbrack and Dill 1983). Both reaction distance (Fig. 10.10) and attack distance (Fig. 10.11) were increasing functions of food width and fish size. Attack distance declined in satiated fish and the probability of ingestion following an attack declined with largest prey. The predicted size composition of a fish's diet based on these relationships was tested with fish captured from the wild, held for 24 h without food to ensure their guts were empty, and then released into cages placed in a stream. Predicted and actual diet corresponded closely, and showed a strong bias towards larger prey.

Feeding behavior often changes with experience and learning in vertebrate predators. Searching often improves via greater reactive distances, higher swimming speeds, and greater path efficiency, while attack latency may decrease and capture success may increase (Dill 1983). The result is a tendency to specialize on the prey that the predator has consumed most frequently in its recent feeding history, with an accompanying increase in foraging efficiency. Hunger can influence predation rate by modifying any of several aspects of predatory behavior. As hunger declines, search behavior also declines owing to changes in movement speed and reactive distance. In addition, the probability that an attack will follow an encounter declines, and handling time of prey tends to increase (Ware 1972). Capture rate consequently varies with hunger level.

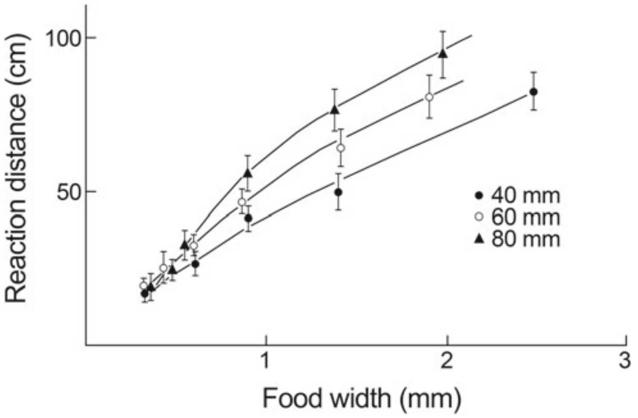

Fig. 10.10 Reaction distance (cm) as a function of prey (stonefly) width (mm) and fish size (40, 60 and 80 mm length) for young coho salmon (*Oncorhynchus kisutch*). Lines fitted by eye. Vertical bars represent 1 SE (Reproduced from Dunbrack and Dill 1983)

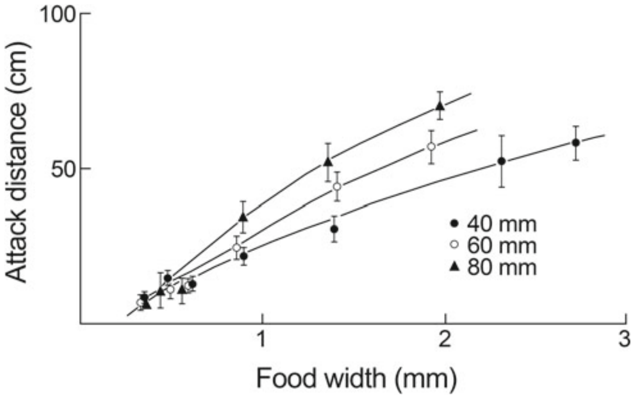

Fig. 10.11 Attack distance (cm) (distance swum by fish from its station to point of capture) as a function of food width and fish length for young coho salmon (*Oncorhynchus kisutch*). Lines fitted by eye. Vertical bars represent 1 SE (Reproduced from Dunbrack and Dill 1983)

Prey of terrestrial origin falling onto the water surface can be an important part of the diet of some stream fishes, especially day-active, visual predators. Based on stomach content analysis and floating surface traps that captured terrestrial infall into small streams of southeastern Alaska, US, juvenile coho salmon consumed approximately equal fractions of terrestrial and aquatic prey (Allan et al. 2003).

Terrestrial inputs may be especially important during summer, when warmer temperatures result in greater energetic demands, and aquatic invertebrates are primarily of small size following adult emergence and reproduction. In the Horonai stream of Japan during July-August, terrestrial prey comprised over 70% of daily biomass consumption by rainbow trout *O. mykiss* (Nakano et al. 1999b; Nakano and Murakami 2001). Trout foraging was greatest at dusk and dawn, when light may limit drift-feeding effectiveness, and terrestrial input peaked near dusk, whereas drift by benthic invertebrates peaked near midnight (Fig. 10.12). Thus, diel periodicity in the availability of terrestrial and aquatic invertebrates, as well as timing of foraging by trout, explain the dominance of terrestrial prey in trout diet. Again, prey size played an important role, as terrestrial invertebrates were larger than aquatic items, and were selectively consumed.

Environmental variables, especially those that affect prey visibility, can significantly modify predation rates. Although visually-dependent predators can feed under quite dim light, prey capture success declines with falling light levels. A light intensity of 0.1 lx, corresponding to late dusk or a full moon, often is the lower threshold for effective visual location of prey (Hyatt 1979). Even within the range we consider daylight, however, gradation in light level can be influential on rates of predation. Wilzbach et al. (1986) compared the feeding of cutthroat trout in pools from forested sections of streams with pools from open (logged) sections. Prey were captured at higher rates in open pools, and artificial shading lowered the capture rate to that observed in shaded pools. Under varying light conditions corresponding to twilight, moonlight, and overcast night conditions, the foraging efficiency of young Atlantic salmon *Salmo salar* in the laboratory was unaffected by current velocity until light levels fell below 0.1 lx, at which point the fish were more efficient at prey capture in slower currents (Metcalfe et al. 1997). When provided a choice of foraging location, juvenile salmon shifted towards slower velocity position as light level declined.

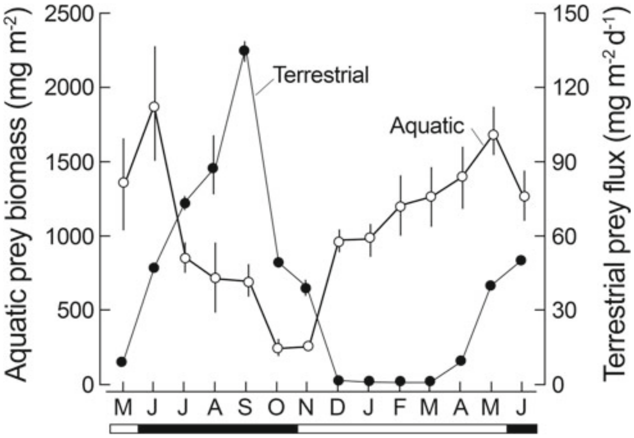

Fig. 10.12 Seasonal variation in prey availability as aquatic invertebrates versus terrestrial infall to the Horonai Stream, Hokkaido, Japan. Aquatic prey biomass estimated from substrate sampling, terrestrial prey inputs from pan traps on the stream surface. Black and white portions of horizontal bars at bottom of figures indicate leafing and defoliation periods, respectively (Reproduced from Nakano and Murakami 2001) © 2001 by The National Academy of Sciences of the USA

While studies of prey capture by fish feeding on surface or water column prey nicely illustrate how size and visibility influence prey capture, predators are opportunistic, shifting their foraging behavior between sit-and-wait and active search. They move between habitats, and exploit prey from the surface, the water column, and the benthos. In a study of prey selection by brook trout, *Salvelinus fontinalis*, Forrester et al. (1994) established trout densities in replicate 35-m long stream sections at either medium or high levels relative to natural densities. Trout fed selectively on larger prey during the daytime, preferring cased caddis larvae and several species of mayflies and stoneflies, but showed no size selection at night. Because cased caddis rarely drift, their consumption presumably reflects benthic foraging. Other prey may have been captured by drift-feeding, and reduced visibility and the resulting smaller visual field at night may explain the absence of size selection at night.

Although less well studied than the salmonids, research into foraging by other stream fishes illustrates some very different feeding modes. Fishes in the family Galaxiidae (Fig. 10.13) are the dominant and most species-rich group of freshwater fishes throughout the cool southern hemisphere, with >50 species occurring in many parts of Australasia, Patagonian South America, and South Africa (McDowall 2006). Galaxiids actively pursue prey at night, apparently detecting prey by disturbing them or by contact, although they also capture prey during the day from a fixed position (McIntosh and Townsend 1995). In Central Europe, the gudgeon (*Gobio gobio*) and stone loach (*Barbatula barbatula*) are benthivorous fish that feed primarily at night and non-visually (Worischka et al. 2015). Principal prey were small bodied, active, and abundant aquatic invertebrates, especially chirononomids and simuliids (Diptera). Visual detection may play a small role in prey selection in the gudgeon, but not in the loach; however, these two predators were broadly similar in diet. They differed in habitat occupation, however. Field video revealed that the gudgeon foraged almost exclusively in pools and was more active at night than during the day, whereas the stone loach used both riffles and pools, and foraged only at night (Worischka et al. 2012).

Feeding from a fixed location on prey items delivered by the current is common in many stream fishes, and is the basis for pioneering efforts to model foraging efficiency based on energy gain from prey consumption and energy expenditure

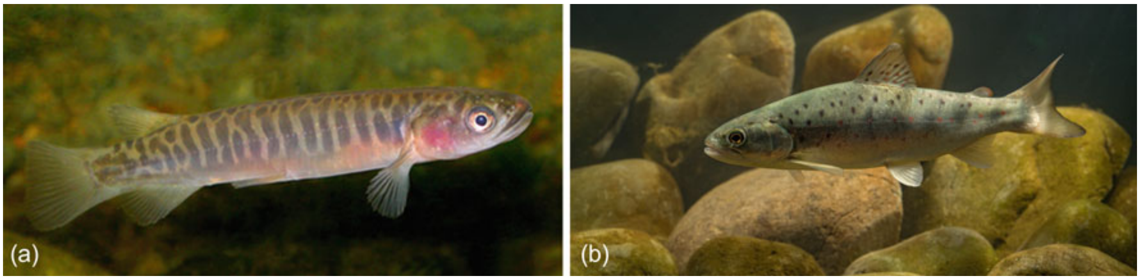

Fig. 10.13 (**a**) a species of galaxias (*Galaxias vulgaris*) from New Zealand. Fishes in the family Galaxiidae are the dominant and most species-rich group of freshwater fishes (with >50 species) throughout the cool southern hemisphere, found in many parts of Australasia, Patagonian South America, and South Africa. (**b**) The brown trout, *Salmo trutta*, native to northern Europe and now common in many streams in the southern hemisphere, frequently restricting or eliminating galaxiids. Photos by Angus McIntosh

in prey capture (Fausch 1984; Hughes and Dill 1990). Foraging theory holds that individuals attempt to optimize their net energy intake (NEI), and thus their growth and fitness, by strategies that provide high energy intake while minimizing energy expenditures. For drift-feeding fish, this translates to selecting locations that maximize prey delivery while minimizing swimming costs, and it further implies that more dominant individuals will successfully compete for preferred locations. On the premise that a drift-feeding fish could optimize its net energy intake by selecting locations in low water velocity near faster currents that deliver abundant drifting invertebrates, Fausch (1984) developed a simple model of positions held by salmonids. Tested in laboratory streams, the growth rate of juvenile trout and salmon increased with NEI, and the rank of NEI at positions held by coho salmon correlated nearly perfectly with their rank in the dominance hierarchy.

Subsequently, Hughes and Dill (1990) developed a more detailed model of position choice by drift-feeding fish in which the number of prey a fish encounters varies with its reaction distance to prey, water depth, and water velocity, while the proportion captured declines with water velocity. Net energy intake is derived from food consumption minus the swimming cost calculated by using water velocity at the fish's focal point. Positions chosen by solitary Arctic grayling (*Thymailus arcticus*) in the pools of a mountain stream in Alaska closely matched Hughes and Dill (1990) model predictions and proved superior to predictions from the Fausch (1984) model, due to more realistic assumptions about the number of prey the fish detected and the influence of water velocity on the prey capture abilities of the fish.

As elegant as this model is, it likely needs further refinement to accurately describe fish foraging behavior. A test of the Hughes and Dill model with brown trout in a New Zealand stream found that reaction distance equations predicted prey size selection well, but the model over-estimated prey capture rates by a factor of two, prey detection averaged only half the expected value, and capture probability decreased rapidly with distance from fish's focal point (Hughes et al. 2003). In addition, trout captured about two-thirds of their prey downstream of the focal point, rather than upstream. Water temperature also may play a role. In experiments with juvenile brown trout at different temperatures, Watz et al. (2012) observed station-holding at temperatures below 10 °C, and a positive relationship between the proportion of time a fish spent holding a foraging station and the fish's capture success when feeding on drifting prey. Above 10 °C, however, trout shifted from a sit-and-wait foraging mode to cruise foraging, achieving nearly equal capture success regardless of foraging mode, and capturing most of the prey encountered. At low temperatures, fish may lack the swimming capacity to pursue prey detected further downstream, compared with their ability in warmer water. The shift from drift to cruise feeding may also compensate for low prey densities because cruising fish search both the water column and the stream bed for food (Fausch et al. 1997; Nakano et al. 1999a). This suggests that foraging models based mainly on drift feeding may need to be broadened to incorporate both feeding modes. An additional energetic cost experienced by drift-feeding fishes is related to pursuit of false food items, such as drifting debris. Using high-definition video to measure the reactions of drift-feeding juvenile Chinook salmon (*O. tshawytscha*) to natural debris, Neuswanger et al. (2014) found that up to 25% of an individual's foraging time was expended in capturing and rejecting inedible particles. This likely represents an energetic cost that varies with environmental conditions, but is not yet built into models of foraging time and energy return.

At present, fish habitat needs are often estimated using physical habitat models based on statistical associations of fish assemblages with simple hydraulic variables such as width and depth, known as habitat suitability curves. As discussed in Chap. 5, there is a growing sense among fisheries managers that such methods fail to represent a mechanistic understanding of fish habitat requirements (Railsback 2016). Further refinement of foraging models has the potential to predict fish habitat requirements based on food supply and net energy intake, thereby generating an improved understanding of larger-scale patterns of stream fish distribution, growth, and abundance.

Discussion of fish foraging behavior would be incomplete without acknowledgement that predators need to be wary of their own enemies. Exclusion of great blue herons (*Ardea herodias*) and belted kingfishers (*Ceryle alcyon*) from sections of two small prairie streams in Illinois, US, resulted in significant increases in medium size classes of two common prey, striped shiners (*Luxilus chrysocephalus*) and central stonerollers (*Campostoma anomalum*) (Steinmetz et al. 2003). As with most predators, fish-eating birds have size preferences that vary among species, avoiding prey that are either too small or too large, but this topic appears understudied. Riparian predators can also present challenges for fishes. Photographic monitoring of rainbow and cutthroat (*O. clarkii*) trout tethered in shallow microhabitats that lacked cover recorded successful captures by riparian predators, including raccoons and eight species of birds (Harvey and Nakamoto 2013). While capture rates likely were higher in this study than is the case with free-swimming fish, they demonstrate that fish in streams are at significant chronic risk from a variety of predators. Of course, habitat choice, including use of cover and locations of greater depth, will influence predation risk. As Power (1984b) showed in streams in Panama, herbivorous fishes avoided shallow-water areas around the margins of pools, resulting in "bathtub rings" of algae.

What a predator eats is often determined simply by an analysis of stomach contents, either by dissection after capture of both invertebrate and vertebrate predators, or non-lethally with fish by forcing water into the stomach with a syringe, flushing out prey. Because the diet of fish often reflects prey availability, which can change seasonally and with habitat, stomach analysis provides only a snapshot of what a particular fish is eating at a particular time. An alternative approach uses stable isotopes of carbon and nitrogen as indirect tracers of fish diets, and because the isotopes are from body tissues, they reflect an integration over time. Compared with stomach analyses, stable isotopes provide time- and space-integrated insights into trophic relationships that can be used to develop models of trophic structure (Layman et al. 2012). The most commonly analyzed elements in food-web analyses are nitrogen (N) and carbon (C). The ratio of ^{15}N to ^{14}N (expressed relative to a standard, δ^{15}N) increases (becomes "enriched") with each trophic transfer, and thus is an estimator of trophic position. The ratio of ^{13}C to ^{12}C (δ^{13}C) differs among primary producers with different photosynthetic pathways (e.g. C3 versus C4 photosynthetic pathways in plants), but changes little with trophic transfers. Because algae primarily use the C3 pathways and many terrestrial plants (and hence allochthonous detritus) are C4, a plot of δ15 N against δ13C for organisms in a food web reveals both trophic position and the relative importance of autochthonous vs allochthonous production within a food web.

The usefulness of stable isotope analysis to identify predator feeding habits is nicely illustrated by a study of four crocodilian species in the central Amazon (Villamarin et al. 2017). Most crocodilians are considered generalist opportunistic predators that feed on any source of protein available, with any diet differences attributable to habitat use. However, the δ^{13}C signature, determined from a claw and small piece of dorsal tail muscle from captured animals, revealed differences in diet resulting not only from habitat selection but also from prey preferences. Mean δ^{13}C values were highest in the headwater species, intermediate in two species of flooded-forest streams and lowest in the species occupying floodplains, reflecting an increasing downstream reliance on aquatic over terrestrial resources. Significant differences were also observed between two co-occurring species of dwarf caiman, *Paleosuchus trigonatus* and *P. palpebrosus*, indicating different prey bases despite habitat overlap.

10.2.1.2 Invertebrate Predators

Relative body size of species within a food web strongly influences trophic relationships, with consequences for resource partitioning, diet breadth, and predator-prey interactions. Most predators consume prey that are smaller than themselves, and at least for invertebrate predators in running waters, on average the mass of their prey is roughly two orders of magnitude less, or about one percent, of the mass of the predator (Woodward and Warren 2007). While ease of subduing prey provides an obvious mechanism, it is instructive to consider each component of a successful predation event. Likelihood of detection may increase with size, and very small prey may not elicit an attack. Attack probability is often thought of as unimodal, around an optimal prey size, although this may not be universal. Capture success may decrease with largest prey, while handling time (and thus the overall rate of obtaining prey) increases for larger prey. Larger species may outgrow predation risk, entering a 'size refuge' at some stage of their life cycle, whereas smaller species may never reach a size where they escape predation.

Although these statements may apply to all predator-prey interactions, they are especially true within invertebrate systems, as is illustrated by the extensive mutual predation and cannibalism seen within the predator guild of Broadstone Stream in southern England (Woodward and Hildrew 2002). The six species (three predaceous midges, a caddisfly, an alderfly, and a dragonfly) exhibited marked size differences, but relative size relationships changed seasonally due to growth (Fig. 10.14). Small predators had the narrowest diets. The overlap in the size of prey consumed was greater when predator sizes overlapped strongly, but declined as predator size diverged (Fig. 10.15). The largest predator, *Cordulegaster boltonii*, was preyed upon only by larger conspecifics, and the smallest, *Zavrelimyia barbatipes*, was eaten by all five of the larger species and by conspecifics. The direction of intra-guild predation could be reversed whenever early instars of large species coexisted with late instars of small species. In this system, clearly, food web structure was influenced mainly by body size relationships, although encounter probabilities and foraging mode also were influential.

Predator foraging mode affects prey vulnerability, interacting with aspects of prey movement to influence localized encounter rates and departures. Mobile prey are likely to flee if able to detect the approach of large, actively searching predators, and so predator impact may be greatest with least mobile prey. This is a complication for cage experiments, which have the potential to overestimate predator impact when predator and prey are confined, and to underestimate whenever prey can escape or colonize from the surrounding environment (Wooster and Sih 1995). For sit-and-wait predators, prey mobility may increase their mortality as a consequence of increased encounter rates. In the Broadstone Stream, predation by the dragonfly *C. boltonii*, a sit-and-wait predator, fell most heavily on mobile mayflies, which were

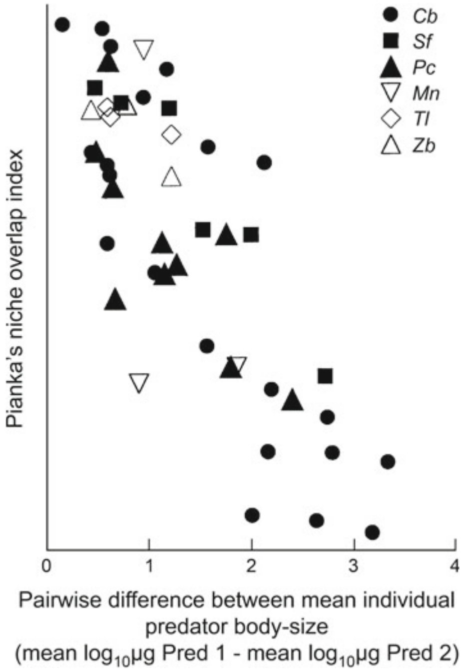

Fig. 10.15 Pairwise dietary overlap among invertebrate predators as a function of differences in individual predator body-size using mean log dry mass of pairs of predators among size classes within each species. See Fig. 10.14 for species codes (Reproduced from Woodward and Hildrew 2002)

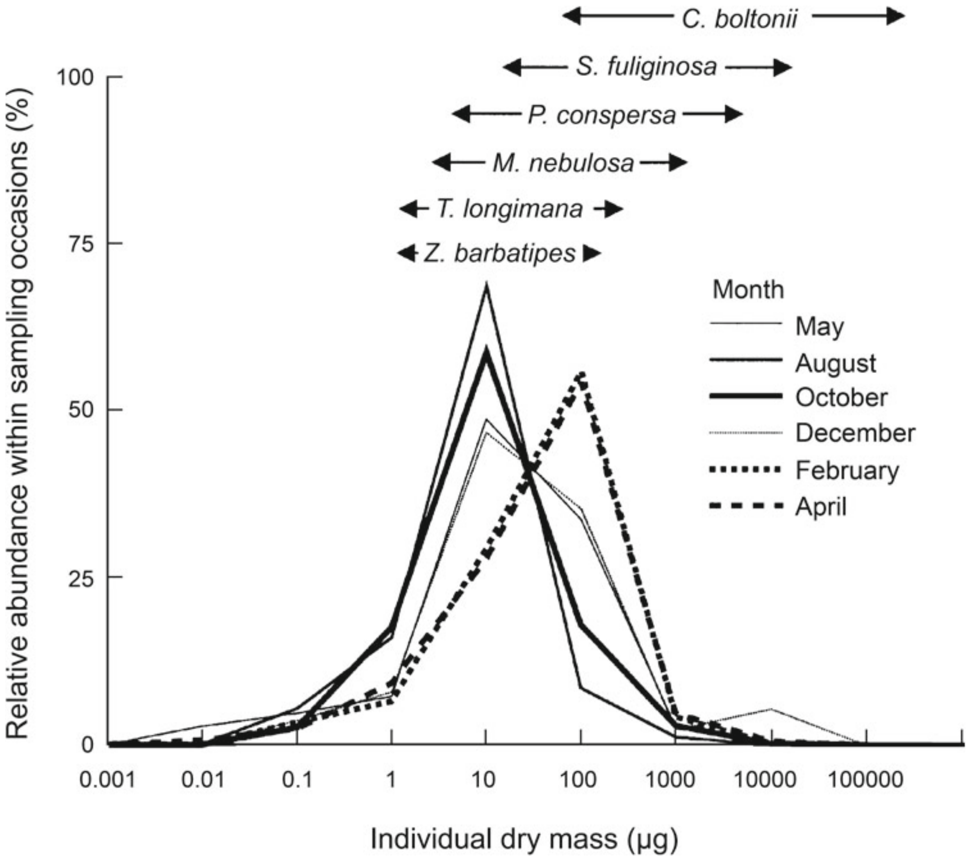

Fig. 10.14 Relative abundance size-spectra of benthic macroinvertebrates in the Broadstone Stream, U.K, on six sampling occasions in 1996–97. The double-headed arrows indicate the size ranges of the six predator species. From largest to smallest the predators include the dragonfly *Cordulegaster boltonii*, the alderfly *Sialis fulginosa*, the caddisfly *Plectrocnemia conspersa*, and three tanypod midges *Macropelopia nebulosa*, *Trissopelopia longimana*, and *Zavrelimyia barbatipes* (Reproduced from Woodward and Hildrew 2002)

not greatly depleted due to high prey exchange rates, but their losses were indeed attributable to consumption rather than flight (Woodward and Hildrew 2002). In the same system, the net-spinning caddis *Plectrocnemia conspersa* also was reported to have the greatest impact on mobile prey (Lancaster et al. 1991). Prey abundance, movement by crawling or drifting, and speed of prey movement and predator attack likely are additional variables affecting encounter rate and capture success with sit-and-wait predators.

The foraging behavior of predaceous invertebrates does not appear to be much influenced by prey availability or prior experience, although it has been suggested that predators aggregate in areas of high prey density (Malmqvist and Sjostrom 1980). However, Peckarsky and Dodson (1980) found that predaceous stoneflies were no more likely to colonize cages containing high prey densities than cages with few prey. Peckarsky (1985) argued that the absence of any aggregative behavior in these predators is explained by the ephemeral nature of prey patches, since highly mobile potential victims like *Baetis* can rapidly disperse. Hunger level did influence which prey were consumed by the stonefly *Hesperoperla pacifica* offered a choice between the soft-bodied, agile mayfly *Baetis bicaudatus*, and the slow and clumsy *Ephemerella altana*, which has a spiny and rigid exoskeleton (Molles and Pietruszka 1983). Starved stoneflies ate mostly *E. altana*, while satiated stoneflies ate both prey in about equal numbers. When freshly-killed prey were offered to starved predators, however, a preference for *Baetis* was evident. The proposed explanation was that starved predators attacked both prey about equally, but with increasing satiation began to restrict their attack only to *Baetis*.

Habitat complexity and the availability of refuges can markedly alter predation rates. Refuges may be absolute, rendering the prey unavailable, but more commonly they serve to reduce the likelihood of encounter and capture. In laboratory trials with two invertebrate predators, four invertebrate prey, and various substrate conditions, Fuller and Rand (1990) showed that all variables affected prey capture rates. *Baetis* was more vulnerable than the other prey (an ephemerellid mayfly, a blackfly larva, and several hydropsychids), probably because its mobility led to high encounter rates. The predators, a stonefly and an alderfly, differed in their predation rates on various substrates due to differences in their sensing of prey with their antennae and with pursuit success. The substrates, which included sand, gravel mixed with pebbles, and artificial turf, resulted in differential capture success via its effects on encounter rates and by facilitating the construction of stronger retreats by some caddis larvae. Although the particular outcomes may be influenced by specifics of the experimental design, such effects of habitat complexity on prey capture probably are common.

10.2.2 Effects of Predation on Prey Populations

10.2.2.1 Direct Effects on Prey Populations

Predators may consume enough prey to reduce prey populations. Often referred to as a direct effect or consumptive effect, predator regulation of prey populations has been investigated by comparisons of predator and prey spatial distributions, by comparisons of prey production with predator consumption, and with field experiments using enclosure/exclosure designs from small cages to large stream sections. Experimental results vary widely, from strong effects of predators on their prey, including increases in benthic algae due to control of grazers; to modest impact on certain, usually large, prey; to no discernible influence at all. Some of this variation appears to be associated with the environmental context, and some may be due to details of experimental design. Most field manipulations are of fish presence/absence, although a few involve invertebrate predators, and the extent of prey reduction attributable to consumption or emigration is not always resolved.

Size classes and species of fishes that are vulnerable to piscivores frequently show an inverse relationship between predator and prey abundances or exhibit non-overlapping distribution patterns. Surveys of fish assemblages at 86 pool sites in tropical streams in Trinidad provided cases where the widely distributed killifish *Rivulus hartii* occurred alone, as well as in various combinations with other species (Gilliam 1993). Its distribution was largely complementary to the piscivorous fish *Hoplias malabaricus*, and its abundance at sites with other species was only about one-third of that predicted from expectations based on *Rivulus*-only pools. In a comparison of 18 streams with trout and six streams without trout in central Finland, *Baetis* densities were five-fold higher in troutless streams, midge larvae showed a non-significant trend towards greater abundance in trout streams, and cased caddis larvae did not differ between the two types of systems (Meissner and Muotka 2006).

Field manipulations have also demonstrated predator impact on prey populations. In a tropical river in northern Australia, macroinvertebrates were roughly twice as abundant in large fish exclusion cages that were approximately 20 m in length and 2–7 m wide (Garcia et al. 2015). Using enclosures with open cobble/gravel bottoms and large-mesh netting that allowed invertebrates to move freely, Dahl (1998) introduced brown trout (*Salmo trutta*) and leeches (*Erpobdella octoculata*) separately and together to compare the influence of a predator selective for large prey, the trout, and one selective for small prey, the leech. Invertebrate size distribution and biomass were reduced in the presence of trout due to a strong effect of trout on the amphipod *Gammarus.* This pattern was due to direct consumption of the amphipod as well as emigration of the amphipod out of the enclosures. Although leeches alone did not reduce prey biomass, their presence skewed prey size distribution towards larger individuals, mainly due to emigration by smaller invertebrates from the enclosures. Whether invertebrate predators can have as strong an impact on prey as vertebrate predators is subject to some controversy, but clearly the influence of the former can be substantial, although the species and size classes affected most likely differ.

Several studies of secondary production of predators and prey have concluded that predators consume a large proportion of the available prey production. For instance, brown trout (*Salmo trutta*) consumed essentially all macroinvertebrate production in a New Zealand stream (Huryn 1996), and macroinvertebrate predators likewise consumed all prey production in a southeastern US stream (Wallace et al. 1997). Although the demonstration that the majority of energy produced at one trophic level is consumed by higher trophic levels is not definitive evidence of either bottom-up or top-down control, it certainly indicates that consumption by predators is the principal fate of the trophic level in question. Estimated prey consumption by stoneflies, the most abundant invertebrate predators present at several sites in a Rocky Mountain stream, was roughly half that attributed to trout, suggesting that the influence of invertebrate predators was less than that of fish (Allan 1983). On the other hand, when fish are absent it seems plausible that invertebrate predators consume all secondary production at lower trophic levels. Indeed, predaceous invertebrates consumed nearly all production by detritivorous invertebrates in a coastal stream (Smith and Smock 1992), and consumption by invertebrate predators also was high in small, fishless streams in the southeastern US (Hall et al. 2000).

As a counterpoint to the above, several predator manipulations have reported only modest or no effects on species composition. Removal of the top predator *Abedus herberti* (Hemiptera: Belostomatidae, the giant water bug) from mesocosms placed in arid-land stream pools in southeastern Arizona, US, had no overall effect on species richness or abundance of invertebrate prey but consistently affected large-bodied species (Boersma et al. 2014). Reaching lengths up to 4 cm, the giant water bug primarily reduced abundances of mid-sized (> 10 mm) predators such as dragonfly nymphs. Similarly, the overall diversity and abundance of aquatic insects colonizing substrate did not differ between cages that were exposed to fish predation, compared with exclusion cages, but the diversity of large (>8 mm) invertebrates increased in the absence of predators (Flecker and Allan 1984). Exclusion of trout from 100-m reaches of a small stream in Finland resulted in significant benefits to large prey, particularly predaceous invertebrates and cased caddis, but *Baetis* mayflies and chironomid larvae were unaffected (Meissner and Muotka 2006). Removal of an entire macroconsumer assemblage of fishes and predatory shrimp from pools in a tropical stream in Hong Kong resulted in negligible impact on benthic invertebrates, although grazing mayflies increased modestly (Ho and Dudgeon 2016). Several studies manipulating trout abundance at both large (Allan 1982) and small (Ruetz et al. 2004; Zimmerman and Vondracek 2007) experimental scale have failed to detect any change in prey abundance, possibly because of high dispersal movements of abundant invertebrate prey.

Whether direct, top-down control of stream invertebrates by predators is strong or weak most likely depends on natural context and experimental design. When predator populations are limited by available habitat or their own predators, they are unlikely to consume enough prey to limit prey populations, and prey dispersal can quickly compensate for local losses. In a trout removal study in a Rocky Mountain stream, US, high drift rates suggested that dispersal may have been sufficient to mask any impact of predation (Allan 1982). The availability of prey external to a coupled predator-prey interaction, as when terrestrial invertebrates supplement fish diet, can reduce predation pressure on benthic invertebrates, and any reduction in that subsidy may result in greater predation pressure on benthic prey. In a forest stream in northern Japan, predation by Dolly Varden charr reduced the biomass of herbivorous aquatic arthropods when terrestrial arthropod input was experimentally reduced by placing greenhouse covers over sections of streams. However, no predation effect was evident on the aquatic arthropods when terrestrial arthropod supply occurred naturally (Nakano et al. 1999b).

Details of experimental design also may influence the outcome of predation experiments, since studies typically use a mesh deemed coarse enough to contain fish yet allow the free flow of water to maintain stream conditions as close to natural as possible and minimize sedimentation within cages. When mesh size is large enough to allow dispersal of aquatic invertebrates and cages themselves are small (i.e., on the order of a few square meters or less) prey dispersal may overwhelm prey consumption. Based on a literature review and several specific studies, Cooper et al. (1990) argued that the magnitude of prey exchange (both immigration and emigration) among substrate patches strongly influences the perceived effects of predators on prey populations. Reported predator effects are strongest in cages using small mesh that confined predator and prey to an enclosed area. When Dahl and Greenberg (1999) measured prey exchange rates and predation effects in a Swedish stream using small enclosures (1.5 × 0.5 × 0.5 m) with either 3 mm or 6 mm mesh, with and without brown trout, predation effects were strongest in the 3 mm cages, which had the lower exchange rate. Beyond revealing a possible bias of experimental design, these findings imply stronger predator effects in pools, where prey replenishment rates are low, compared with fast-flowing stream sections, where prey dispersal and colonization tend to be higher. These studies provide further evidence that predation can reduce prey within cages directly, by consumption, and indirectly by inducing emigration and predator avoidance. The importance of these two mechanisms appeared to vary among taxa, likely reflecting taxon-specific differences in mobility, vulnerability, and response to predator cues. The non-consumptive effects of predation are seen in a number of predator-avoidance responses of prey that act to reduce the direct, consumptive influence of predators on their prey, often exacting a cost in reduced energy intake in both predator and prey populations.

10.2.2.2 Non-consumptive Effects of Predation

Exposure to risk of predation is a common consequence of foraging and other activities, and thus individuals will benefit from adaptations that minimize predation risk while maintaining energy intake. Prey species may respond to a predator's presence by escape behaviors, by becoming increasingly nocturnal, or by altering growth and development. Referred to as non-consumptive effects or indirect effects, they provide the obvious benefit of immediate survival, but may result in foregone foraging and thus exact a cost in future growth and fecundity. Some avoidance mechanisms operate regardless of the physical proximity of predator and prey and serve to reduce the likelihood of initiation of an attack, whereas others function to foil attack and capture. Anti-predatory traits can be fixed, such as protective armor or invariant nocturnal activity, or induced by the presence of the predator, such as fleeing after tactile or visual contact or perceiving the ‘scent of death’ when water-born chemicals reveal a predator's presence (Kats and Dill 1998; Preisser et al. 2005). Flexible predator avoidance requires some ability to assess risk and make an escape, and so fixed responses may be favored when those conditions are not met or the cost in lost foraging opportunity is modest. Because predation can rarely be entirely ignored or eliminated, threat-sensitive predator avoidance behaviors should be a widespread solution to the tradeoff between foraging and avoiding being eaten.

Many characteristics of prey can reduce their vulnerability to predators, including small size, nocturnal or crepuscular behavior, use of interstitial spaces, body shape and armor, and so on, although it may not be certain whether those traits have evolved as anti-predator defenses. Mayfly larvae exposed to predaceous stoneflies (*Megarcys signata* and *Kogotus modestus*) in microcosms differed in their vulnerability and responses to predator-prey encounters (Peckarsky 1996). Soft-bodied *Baetis*, an abundant and favored prey, escaped by entering the drift, whereas *Ephemerella*, morphologically defended by a thick exoskeleton, shows no avoidance behavior. Anti-predator responses are also common in fish and amphibians of running waters. Young fish may rely especially on predator avoidance, while older fish may experience reduced predation risk due to size, defensive armor and spines, olfactory cues, and learning (Fuiman and Magurran 1994; Kelley and Magurran 2003). A review of 43 studies of predator–prey fish interactions in lotic systems found that predators caused prey fish to move to habitats of reduced predation risk, such as shallower margins within a given macrohabitat, and in the opposite direction to avoid predation by terrestrial predators. In addition, prey reduced their overall activity and foraging in the presence of predators, resulting in slower growth rates. In laboratory trials, young coho salmon *Oncorhychus kisutch* offered houseflies as prey reduced reaction and attack distances and shortened attack time in the presence of a model rainbow trout, compared to young salmon foraging in the absence of threat (Dill and Fraser 1984). Moreover, the responsiveness of young coho salmon to the model was reduced by higher hunger levels and the presence of a competitor. Anti-predator defenses are found in some amphibians, usually based on palatability or use of chemical cues for avoidance (Kats et al. 1988). Those lacking these defenses are largely restricted to breeding in temporary pools that lack fish.

The downstream transport of benthic invertebrates and its pronounced nocturnal periodicity have fascinated stream ecologists since early researchers, impressed by the quantities of invertebrates drifting downstream, wondered how benthic populations could persist in the face of constant unidirectional losses. Known as the “drift paradox” (Muller 1963; Waters 1972), explanations centered on whether compensatory upstream movement sufficed for population persistence or, alternatively, if drift represented surplus production in excess of carrying capacity. It is now apparent that compensatory upstream movements are modest and depletion of upstream populations is not observed, suggesting instead that drift largely represents small-scale movements important for individual habitat selection and distribution, but with little discernible influence on overall population dynamics of stream invertebrates (Naman et al. 2016).

The nocturnal periodicity of invertebrate drift is best interpreted as an evolved response to risk from predators whose visual field is greatest in daylight. Evidence that nocturnal periodicity varied among size classes and taxa in accordance with predation risk, so that smaller, less vulnerable individuals were nearly aperiodic while larger, more vulnerable size classes and taxa were nocturnal, strongly indicates that nocturnal drift is an adaptation to reduce predation (Allan 1978). Patterns in drift behavior of mayflies in a series of Andean streams provides additional evidence that nocturnal periodicity is a relatively fixed behavioral response to risk of predation by drift-feeding fishes (Flecker 1992). Mayfly drift was primarily nocturnal in piedmont streams with natural populations of visually hunting predators, but was aperiodic in mountain streams that historically lacked drift-feeding fishes. However, where rainbow trout have been introduced to naturally fishless Andean streams, the mayfly *Baetis* exhibited strong nocturnal peaks in drift, suggesting a rapid evolutionary response to an exotic predator. Indeed, nocturnal drift became more pronounced along a gradient of predation regimes (Fig. 10.16), and was observed even when fish were experimentally excluded, suggesting that nocturnal activity has evolved as a fixed behavioral response to predation. In a comparison of fishless and fish-bearing streams in the Rocky Mountains, Colorado, US, the ratio of night:day drift numbers for all mayfly taxa was near 1:1 in fishless streams and near 10:1 for several mayfly taxa in streams with trout (McIntosh et al. 2002).

Why aquatic insects enter the drift is not fully resolved, because entry could be due to accidental dislodgment resulting from foraging movements and turbulence, referred to as passive drift (or catastrophic drift at substrate-mobilizing flows); or entry could be deliberate, to depart from an unprofitable foraging location, avoid benthic predators, or depart from unfavorable abiotic conditions. The strong nocturnal periodicity of drift suggests that at least the nighttime component reflects a trade-off where daytime foraging is restricted to reduce predation risk from drift-feeding fish. Nocturnally foraging benthic predators such as stoneflies may also induce drift entry, as Hammock et al. (2012) observed when the perlid stonefly *Doroneuria* was added to 2-m long channels placed within a fishless stream, relative to control channels that lacked the stonefly. Hydraulic conditions, including turbulence and back eddies, may contribute to dislodgment at any time (Oldmeadow et al. 2010).

Chemical cues (kairomones) are chemicals emitted by an organism that alert prey to the presence of a predator, and predators to the presence of prey. Many freshwater fishes release chemical cues into the water following mechanical damage to epidermal tissues, which serve as a warning to conspecifics and an attractant to predators. In streams of Trinidad, the pike cichlid *Crenicichla alta*, a solitary, visually foraging ambush predator, increased its presence in the vicinity of damage-released chemical cues from its preferred prey, the guppie *Poecilia reticulata* (Elvidge and Brown 2012). Illustrating that cues influence prey as well as predator, lab-reared guppies exposed continuously to chemical cues emitted by *C. alta* strongly reduced food intake in the presence of predator cues, relative to

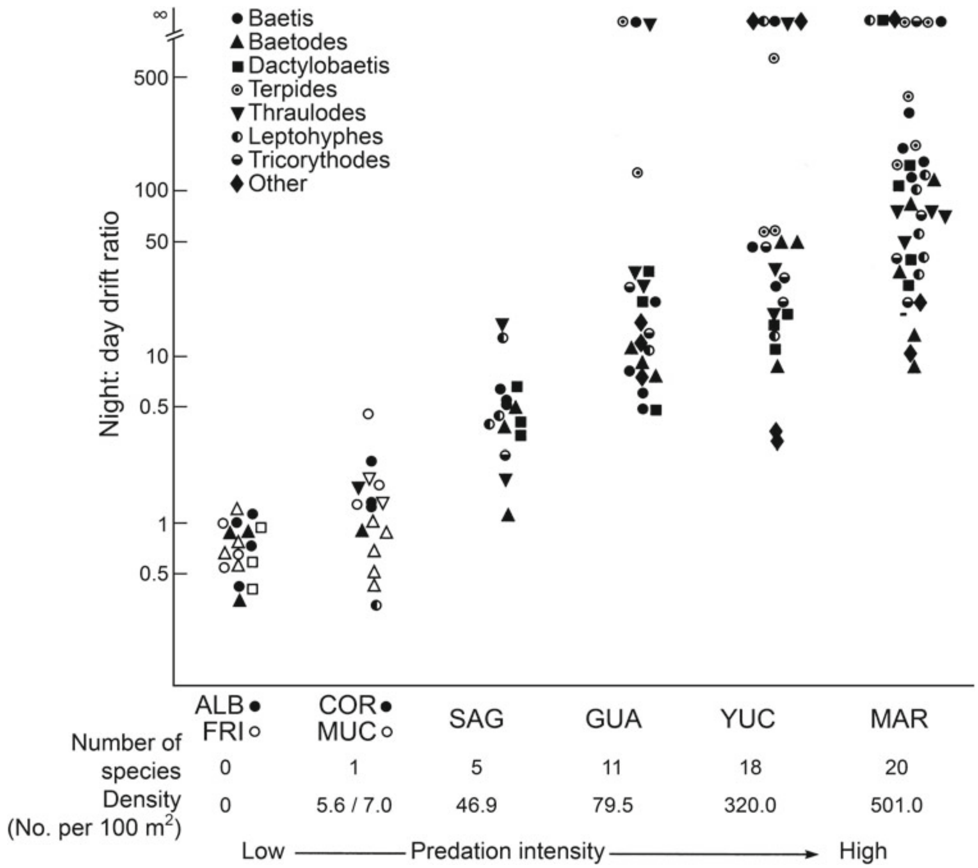

Fig. 10.16 Night:day drift ratio of mayfly drift densities from a series of streams in the Venezuelan Andes representing a gradient from low to high predation. Note that drift is greater by day in high elevation streams lacking drift-feeding fish (Rio Albarregas [ALB] and Quebrada La Fria [FRI]) compared to nearby streams containing introduced trout (Quebradas Coromoto [COR] and Mucunutan [MUC]) (Reproduced from Flecker 1992)

individuals reared in the absence of cues, but assimilated nutrients more efficiently, indicating an induced physiological shift (Dalton and Flecker 2014).

Studies show that mayfly larvae can respond to trout chemical cues by altering behavior and development. When water from holding tanks containing trout was added to microcosms with *Baetis* larvae, nocturnal drift was substantially depressed relative to controls (McIntosh and Peckarsky 2004). In a Rocky Mountain stream containing brook trout and presumably fish odor, release of water containing brook trout immediately upstream of drift nets resulted in a rapid decline in the drift of larger individuals of the mayfly *Baetis*, and an increase in numbers of smaller individuals (Mcintosh and Taylor 1999). The increase in drift by smaller size classes is unexplained, but could reflect an evolved behavior to exit locations of high predation risk prior to reaching a more vulnerable size. Chemical cues from the nocturnal and benthivorous gudgeon *Gobio gobio* suppressed activity of the mayfly larvae *B. rhodani* (Schaffer et al. 2013) and the amphipod *Gammarus pulex*, but amphipods did not react to stone loach *Barbatula barbatula*, which poses less predation risk (Szokoli et al. 2015).

Faster development and maturation at a smaller size appears also to be a response induced by fish "odor". *Baetis* mayflies just prior to emergence are easily identified from their enlarged, darkened wing pads. A survey of size of mature larvae in streams in the Rocky Mountains of Colorado, US, revealed that size at metamorphosis of summer generation *Baetis* was smaller in fish streams than in fishless streams (Peckarsky et al. 2001). This was interpreted as evidence that larval development was accelerated where predation risk was greater, resulting in metamorphosis of younger and smaller individuals. Because fecundity increases with body size, accelerated development likely incurs a cost in future reproduction relative to extended development and larger size at metamorphosis in safe environments. Similarly, field surveys of streams in central New York, US, found that *Ephemerella* mayflies emerged earlier and at smaller sizes in streams with high relative densities of fish, compared to streams with low fish abundance (Dahl and Peckarsky 2003). Laboratory rearing experiments showed that *Ephemerella* larvae exposed to fish chemical cues likewise exhibited faster larval development and smaller size at maturity compared to no such cue, indicating an inducible change in development associated with perceived predation risk.

In closing, predation in stream ecosystems unquestionably exerts a direct influence upon prey populations. Predator foraging mode and prey vulnerability result in differential predation rates that constitute a strong force driving adaptations to minimize predation risk. In some circumstances, predators clearly are able to exclude prey species from certain habitats or markedly reduce their abundance. The immediate effects are lost foraging opportunity and reduced growth rates, or direct mortality, which affects some size classes and species more than others. Because the prey themselves are consumers of other animal or plant resources, the potential exists for predation to create top-down trophic cascades and indirectly affect other species in the food web. In fact, some of the most dramatic effects of predation in lotic ecosystems are revealed in far-reaching cascades, offering convincing evidence that predation is a strong force shaping biological communities.

10.3 Competition

Competition occurs when members of the same or different species utilize shared resources that are in limited supply, thereby reducing one another's individual fitness and population abundance through the depletion of those resources. This definition encompasses two mechanisms of competitive interaction. Exploitation (also termed indirect) competition involves the depletion of shared resources such that another individual is disadvantaged. Interference or direct competition usually is of an aggressive nature, for instance when one individual excludes another from a preferred habitat and foraging location. Competition has long been viewed as a challenge to species coexistence, requiring sufficient differences between species to prevent competitive exclusion. Thus, niche specialization becomes a key consideration in community assembly, a topic we return to in Chap. 12. Competition has been demonstrated in many different settings, however, and when it occurs it often is asymmetrical, with one species able to exclude a second species, which persists by occupying habitats or using resources largely unutilized by the superior species (Begon et al. 2005). Competition may be less evident a force than predation and herbivory, perhaps because it acts more gradually. In addition, competition may often be diffuse, emanating from many species rather than just a pair-wise interaction.

A rigorous demonstration of competition generally requires evidence of an adverse effect of numbers of one population upon the abundance, growth, or survival of individuals of another population under reasonably natural conditions, and also some insight into the mechanism driving the competitive interaction. However, many studies either document some overlap in resource use, from which competition is inferred, or some differences in resource use, from which niche partitioning is inferred. Although such investigations must be viewed as weak evidence for competition, they make up a large portion of the existing literature. We shall first consider the evidence in support of resource partitioning, and then look to other lines of evidence including experimental and natural comparisons. Finally, since unrestrained competition ultimately should result in the elimination of all but the best competitors, it is necessary to ask how commonly and under what conditions this situation occurs. Harsh conditions imposed by abiotic factors, floods in particular, appear to be important in counteracting strong competition in a number of instances, and biotic interactions are likely to be primary only under environmentally benign conditions.

10.3.1 Resource Partitioning

Resource overlap typically is evaluated based on similarities between individuals along three major axes: food, habitat, and time (season or time of day) when the organism is active. The evidence from many studies of resource partitioning, encompassing a variety of taxa in both aquatic and terrestrial settings, indicates that habitat segregation occurs more commonly than dietary segregation, which in turn is more common than temporal segregation (Schoener 1974). Schoener also reported a tendency for trophic separation to be of relatively greater importance among aquatic organisms. Evidence of food specialization historically has been obtained from inspection of gut contents; thus, it matters a great deal whether food items fall into easily distinguished categories. Not surprisingly, food partitioning is reported more commonly from studies of grazers and predators than of detritivores. However, stable isotope analysis of food items and consumer tissue is providing new insights not only into food consumed but also assimilation and growth (Aberle et al. 2005; McNeely et al. 2007). Fish and invertebrates both have been studied extensively from a resource partitioning perspective, but the literature for aquatic plants and benthic algae is scant.

10.3.1.1 Algae

Few studies explicitly address competition between species of algae in lotic ecosystems. It is well established that algal abundance and species composition in artificial streams change in response to adjustments in nutrient, light, or current regime, and assemblages also undergo succession under a particular environmental regime. Many field studies describe shifts in algal dominance associated with changing environmental conditions. The tendency for filamentous green algae to dominate under high light levels is suggestive of a competitive advantage, while their scarcity under low light regimes may be due to the reduced pigment diversity of chlorophytes relative to other common stream algae (Steinman and McIntyre 1987). In comparing the influence of nutrient availability in the water column versus nutrient diffusing substrates, Pringle (1990) observed the diatoms *Navicula* and *Nitzschia* to dominate the overstory and interfere with the establishment of understory taxa *Achnanthes* and *Cocconeis*. Because nuisance blooms of the invasive benthic alga *Didymosphenia geminate* showed a negative correlation with densities of native algal taxa, predominantly of other diatoms that formed thick filamentous mats, Bray et al. (2017) interpreted this as interference competition. Expression of this apparent effect of competition with native taxa varied with nutrient treatments and water velocity. Considering the diversity of periphyton species and variety of growth forms (Fig. 6.1), and the likely competition for substrate space and access to light, future studies of individual algal species may be expected to provide stronger evidence of the importance of competitive interactions within assemblages of benthic algae.

Algae potentially may compete with heterotrophic bacteria within biofilms for access to nutrients, although co-occurrence potentially is mutually beneficial, as when bacteria utilize dissolved organic carbon (DOC) released by photosynthesizing algae, and bacterial breakdown of organic matter releases nutrients important to algae. However, when other sources of labile DOC are present or when algae are light- or nutrient-limited, bacteria are less likely to utilize algal-generated DOC and may instead compete with algae for inorganic nutrients. Rier and Stevenson (2002) tested the latter possibility by experimentally manipulating light levels and using nutrient diffusing substrates to release inorganic nutrients and/or glucose in an oligotrophic stream located in Kentucky, US. They found no evidence that algae were negatively affected by competition with bacteria for nitrogen and phosphorus, nor that bacteria were using algae as a carbon source. They speculated that algae serve as a substrate for bacterial colonization, and that is the basis for their positive association.

10.3.1.2 Invertebrates

Many studies document habitat partitioning among stream-dwelling invertebrates. Temporal separation of life cycles over seasons is frequent among the univoltine (one generation per year) insects of temperate streams, and differences in diet are reported principally in animals that consume easily categorized food items. The distribution and abundance of filter-feeding caddisfly larvae provide an attractive system for the study of resource partitioning, as they utilize the common resource of FPOM, require space to attach their nets, and have seemingly ample opportunity for resource partitioning via differences in the mesh size of capture nets and location of attachment. Indeed, differences in food particle size consumed (Wallace et al. 1977), microhabitat distribution (Hildrew and Edington 1979), longitudinal distribution (Lowe and Hauer 1999), and life cycle (Mackay 1977) have each been demonstrated. The instars of a species also differ in habitat use, and their preferred current velocity typically increases over their development (Osborne and Herricks 1981). On the other hand, it does not appear that either food or space commonly is limiting to co-occurring caddis larvae. After estimating the size fraction captured by six filter-feeding caddis larvae as well as total availability of organic particles, Georgian and Wallace (1981) found no evidence that food was limiting or that resource partitioning occurred. The size fractions captured showed very high overlap, and amounted to only about 0.1% of available FPOM.

Although it remains unclear whether competitive interactions among species of filter-feeding caddis larvae frequently limit their distribution and abundance, this guild nonetheless illustrates resource partitioning along multiple dimensions. Some species clearly differ in net dimensions, current, and other microhabitat preferences, and in temperature adaptations that determine larger-scale spatial segregation. Detailed analysis of microhabitat use by filter-feeding caddis larvae in lake outlet streams in northern Finland revealed differences among instars and species, particularly in their association with moss and with a hydraulic metric, the Froude number (Muotka 1990). *Polycentropus falvomaculatus* was a microhabitat generalist but three species of *Hydropsyche* (*H. augustipennis*, *H. pellucidula*, and *H. saxonica*) were more specialized. It has been suggested that larger species with their larger mesh sizes are suited to higher current velocities and also to capture larger food items, and smaller mesh sizes might function best in slow currents (Alstad 1987), but Muotka (1990) found only partial agreement with this expectation, and in one study the species with the smallest mesh net was most abundant at the highest velocities (Wallace et al. 1977).

Although temporal segregation apparently is less common than habitat or diet partitioning across diverse taxa (Schoener 1974), numerous examples from temperate running waters illustrate a distinct seasonal succession among closely related species. Co-occurring species of stoneflies in the genus *Leuctra* and family Nemouridae in small streams of the English Lake District display staggered life cycles that minimize the temporal overlap in their resource demands (Elliott 1987a, b). The periods of maximum larval growth were sufficiently out of phase among five species of riffle-dwelling *Ephemerella* mayflies to ensure at least ten-fold size differences on any given date between the most closely related species (Fig. 5.14). Highly synchronized, non-overlapping life cycles among presumed competitors are not always the rule, however. Of six leptophlebeid mayflies in a New Zealand stream, only two had reasonably well-defined growth periods, and overlap of life histories was pronounced (Towns 1983). As with resource partitioning along microhabitat and food axes, temporal specialization likely is offset by the advantages of flexible habits and life cycles.

To evaluate whether temporal partitioning should be attributed to competition, Tokeshi (1986) developed a null model of expected overlap by assuming that species' life cycles were distributed independently of one another throughout the year, with the constraint that most growth should occur during favorable seasons. For nine species of chironomid larvae living epiphytically on spiked water-milfoil and consuming a similar diet of diatoms, actual overlap of life cycles was greater than expected by chance alone. Since this result is the opposite of that expected in temporal partitioning, it appears that all nine species were tracking seasonal peaks in resource abundance. Competition, if it occurred, was not manifested in temporal partitioning.

10.3.1.3 Fishes

Resource partitioning within fish assemblages has received a great deal of study, and as with macroinvertebrates, extensive segregation can be documented along the axes of diet, habitat, and time. In a review of some 116 such studies conducted primarily with salmonids of cool streams or small, warmwater fishes of temperate regions, Ross (1986) found that segregation along habitat and food axes was about equally frequent while temporal separation was less important. However, even among similar faunas the importance of space, food, and time axes varied considerably. Although the resource partitioning perspective is upheld in many studies, other researchers report greater overlap and attribute co-occurrence to a combination of individual specializations and the importance of environmental variation in mitigating competitive interactions.

Studies of darters and minnows in North America provide examples of low overlap in species distributions or in microhabitat and feeding position at a single locale. Eight species of cyprinids that co-occurred in a Mississippi stream showed considerable microhabitat segregation with respect to vertical position in the water column and association with aquatic vegetation (Baker and Ross 1981). Only two species failed to separate on these two axes, and one was the only nocturnal feeder in the assemblage. Direct observation by snorkeling in streams of West Virginia, US, found evidence of habitat partitioning by depth, substrate size, and water velocity for 10 darter species. *Percina* typically occurred in the water column, whereas species of *Etheostoma* were benthic and segregated by occurring under, between, and on top of rocks (Welsh and Perry 1998). Moyle and Senanayake's (1984) study of an even more diverse group of fish in a small rain forest stream describes a highly structured assemblage with minimal overlap based on fish morphology, habitat use, and diet.

The extent of resource overlap versus partitioning is likely to vary with food availability owing to opportunistic feeding when certain prey are very abundant. Seasonal changes in diet overlap are well illustrated by Winemiller's (1989) study of nine species of piscivorous fish that were abundant in a lowland stream and marsh habitat in western

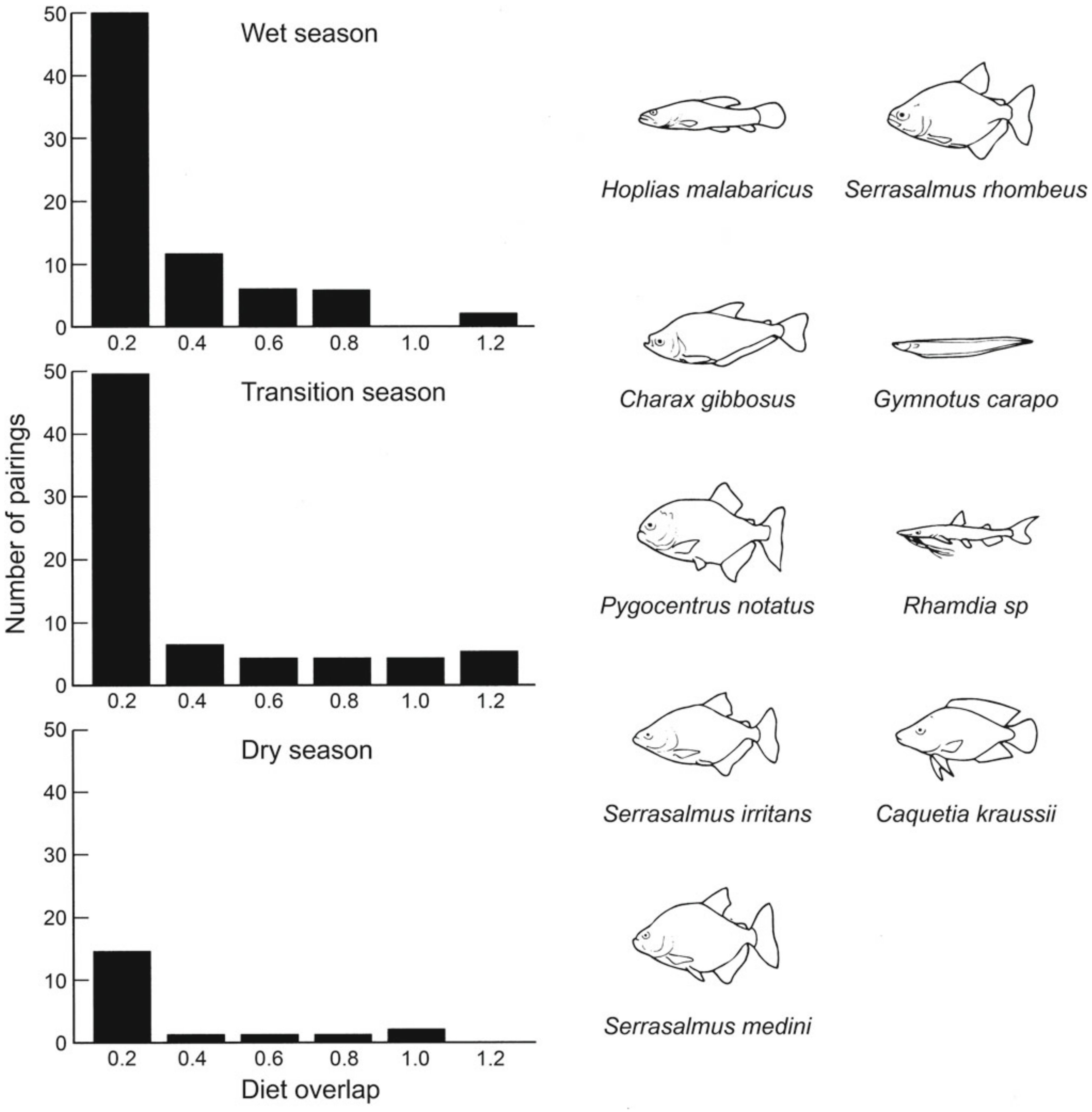

Fig. 10.17 Frequency histograms of dietary overlap exhibited by each of nine piscivorous fish during different seasons at a lowland creek-and-marsh site in Venezuela. Wet season lasts from May to August, transition season from September to December, and dry season from January to April. Diet overlap was computed from pairwise comparisons of ingested prey after converting prey abundance to volume as an approximation of biomass. Dry season data are less extensive because not all species were present and many had empty guts. Over half of overlap estimates were <0.10 (Reproduced from Winemiller 1989)

Venezuela. Members of this guild exhibited substantial resource partitioning in food type, food size, and habitat. Of the possible 72 species combinations among the nine piscivores, only one pair of fin-nipping piranhas exhibited substantial overlap on all three niche dimensions. For the most part, diet overlap of pairs of piscivore species within their feeding guild was low (Fig. 10.17). Highest overlap occurred during the wet season when prey were abundant and lowest overlap occurred during the transition season when prey were least available. Thus, despite the opportunities for competition in this species-rich tropical system, food resource partitioning was widespread. Winemiller (1991) concluded that the higher species diversity of tropical fish assemblages relative to temperate assemblages was paralleled by higher ecomorphological diversity (body and mouth shape, dentition, etc.), which facilitates niche partitioning and reduces competition.

Some studies of habitat partitioning among stream fishes have reported segregation between groups of species occupying distinct microhabitat guilds but considerable remaining overlap at the species level. In an observational field study of six minnows in an Ozark stream, using the habitat variables of water depth, current, substrate, vertical and lateral position of the fish, and their use of pools, riffles, and glides, Gorman (1988) found a clear separation between species occupying higher versus lower water column position but considerable overlap among species within those two categories. The fishes of Coweeta Creek, North Carolina, were separable into three microhabitat guilds: benthic, lower, and mid-water column, but differences in microhabitat use between species within these guilds were not easily distinguished (Grossman et al. 1998). This is interpreted as evidence that environmental variation is more influential than resource availability in limiting population densities of stream fishes, as several authors have argued (Gorman 1988; Baltz and Moyle 1993). In this view it is advantageous that fishes exhibit flexibility and overlap in their use of resources, and assemblage structure reflects the combined influence of environmental variation, particularly in hydrology, together with differences among species in their individual ecology.

Further evidence of competitive interactions among stream fishes can be found in the many examples of novel species combinations that result from invasions, range expansions, and intentional introductions. The many introductions of salmonids to benefit recreational fishing provide numerous examples where a non-native has displaced ecologically similar species over wide regions. Size advantage, aggressiveness, and possibly differences in foraging adaptations as well as predation by the invader on the native species are underlying mechanisms. Relative to native consumers, invaders may possess a novel feeding mechanism, a broad feeding niche, greater energetic efficiency in transforming prey resources into consumer biomass, and greater resilience in the face of natural disturbances (Simon and Townsend 2003).

The widespread replacement of southern hemisphere native galaxiids, which are mostly benthic foragers that use mechanical cues to feed both day and night, with day-feeding, northern hemisphere trout, illustrates this well (Fig. 10.13). Fishes in the family Galaxiidae are the dominant and most species-rich group of freshwater fishes across the cool southern hemisphere, with >50 species in Australasia, Patagonian South America, and South Africa (McDowall 2006). Invasion of cold temperate, southern hemisphere, fresh waters by rainbow trout and brown trout is associated with widespread decline and extirpation of native fish species. Brown and rainbow trout have been widely introduced in Australia and New Zealand, where they are the mainstay of a highly successful sport-fishing industry (Crowl et al. 1992). In a survey of 198 sites of the Taieri River Drainage in the South Island of New Zealand, both species co-occurred in only nine sites, and then at significantly lower densities (Townsend and Crowl 2006). A survey of 54 small streams on an island in Chilean Patagonia found rainbow trout (*Oncorhynchus mykiss*) to be more widely established than brown trout (*Salmo trutta*), and the two invaders have had different impacts (Young et al. 2010). *Aplochiton*, a trout-like, drift-feeding native species of the Galaxiidae, inhabits uninvaded streams and co-occurs with rainbow trout, but has been nearly eliminated where brown trout occur. Rainbow trout may be more widespread because of greater dispersal tendencies or broader environmental tolerances, but brown trout may have the greater impact where they occur due to a greater reliance on piscivory. The eventual outcome for *Aplochiton* is uncertain: they may persist where habitat or other aspects of the invader's niche limits its abundance, or gradually become extirpated as non-native trout continue to colonize remaining locations.

In many streams of western North America, native bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarkii*) have been replaced by the now widespread brook trout, *S. fontinalis,* introduced from eastern North America, and brown trout from Europe. And in mountain streams of the Pyrenees in southwest France, rainbow trout native to western North America have negatively affected habitat use, growth, and survival of native brown trout (Blanchet et al. 2007). Aggressive encounters among salmonid species and between size classes are well known, providing the mechanism for direct or interference competition. Fausch and White (1981) recorded the daytime positions of brook trout in the presence of brown trout, which is the behaviorally dominant species, and then removed brown trout from a section of a Michigan stream. Brook trout subsequently shifted to resting positions that afforded more favorable water velocity characteristics and greater shade, and this habitat shift was greatest in the larger individuals. Such interactions are not limited to the salmonids, of course. A study of interactions between a native fish, the rosyside dace (*Clinostomus funduloides*), and an invasive, the yellowfin shiner (*Notropis lutipinnis*), collected from an Appalachian stream in the southeastern US, found that larger fish dominated in intraspecific interactions, and the invasive species in interspecific interactions (Hazelton and Grossman 2009). However, velocity and turbidity influenced habitat position and aggressive encounters, illustrating the role of environmental context in mediating species interactions.

A common distribution pattern among many now-rare native salmonids is to be restricted to high-elevation headwaters, with replacement by nonnative fishes in lower-elevation reaches. This has led to an hypothesis of temperature-mediated competition, whereby high-elevation species are considered to be superior competitors at cold temperatures, excluding low elevation species, while the reverse is thought to be true at low-elevation, warmer sites. In a laboratory study of growth, feeding, and aggression of bull and brook trout at different temperatures, McMahon et al. (2007) reported a clear metabolic advantage for brook over bull trout at warmer temperatures, but bull trout, increasingly restricted to cool headwaters, did not gain a competitive, size, or survival advantage over brook trout at colder temperatures. However, the competitive advantage of brook trout is reduced at low temperatures, and that, along with complex habitat and proximity to nearby bull trout populations, may explain bull trout persistence. Similarly, in a field study measuring growth and condition (a measure of body mass at a given length) of cutthroat and brown trout at six locations along the thermal gradient of the Logan River, Utah, US, McHugh and Budy (2005) found that brown trout negatively affected cutthroat trout growth and condition, but the converse was not supported. Temperature had little effect on the outcome when both species co-occurred, but precluded brown trout invasion of upper elevations. These studies lend weight to the view that abiotic factors and physiological limits of the downstream species thus determine the upstream boundary of its distribution, and reversals in dominance in which the upstream species is demonstrably the better competitor at colder temperatures rarely occur.

Environmental conditions can strongly influence not only the local distribution of a non-native species, but also its ability to establish populations in a novel environment. The invasion success of rainbow trout, one of the most widely introduced species worldwide, is strongly influenced by a match between timing of fry emergence and months of low flood probability. It has been most successful where hydrologic regimes are most similar to its native range, and only moderately successful or has failed where spring or summer flooding has hampered recruitment (Fausch et al. 2001).

In closing, the extensive literature on resource partitioning clearly demonstrates that species differ in their habitat use, food capture abilities, and timing of activity or growth. These are in effect descriptions of the specializations that constitute a species' niche. Such differences constitute weak evidence of competition, as they do not resolve whether species adversely affect one another, or whether these examples of niche segregation reflect ecological specializations acquired and fixed over the species' evolutionary history. It is for these reasons that recent work has focused on more rigorous tests, typically involving experiments under fairly natural conditions, and we now consider such studies.

10.3.2 Experimental Studies of Competition

Competitive interactions can be manipulated in the laboratory or in the field, conditional on the ingenuity of the investigator to construct an experiment that allows realistic interactions and reveals the mechanisms involved. Laboratory experiments usually offer the greatest experimental control and can be particularly useful in demonstrating the potential for competition and in identifying mechanisms. Field experiments offer greater realism—at least in principle—although they too have artifacts and their outcomes may be influenced by the relatively small scale and short timeframe of the typical field study. Investigators often have used a combination of laboratory and field experiments, and in some cases have exploited natural comparisons or unusual environmental events to provide evidence of competitive effects at large scale and under natural conditions.

Interference competition is well documented in space-limited taxa of invertebrates. Large size almost invariably conveys an advantage, and the loser may be injured or cannibalized. In the latter instance the line blurs between competition and predation. Larvae of the netwinged midge (*Blephariceraa*) and black flies (Simuliidae) compete for space on stone surfaces in swift-flowing small streams, even though the former feed on attached periphyton and the latter are primarily suspension feeders. Their densities were inversely correlated in a California stream, and behavioral observations of interactions revealed that larval black flies "nipped" at *Blepharicera* within reach, disrupting their feeding (Dudley et al. 1990). *Blepharicera* spent significantly less time feeding in the presence of black fly larvae, compared to when the investigators removed all simuliids within a 5 cm radius. Aggressive competitors such as caddis larvae affect other species by multiple mechanisms including interference, predation, behavioral avoidance, and by modifying flow patterns (Hemphill 1988). Small-scale density manipulations of *Hydropsyche siltalai* illustrate the multiple pathways of its influence in a lake outlet stream in north Sweden (Englund 1993). The presence of *H. siltalai*, a net-spinning filter feeder that aggressively monopolizes space, resulted in reduced numbers of the mayfly *Ephemerella ignita* and the black fly *Simulium truncatum*, and increases in the free-living, predatory caddis *Rhyacophila nubila* and chironomid larvae. Direct mortality due to predation was the primary cause of declines, although hydropsychid nets likely also interfere with the attachment and feeding of simuiliid larvae. Increased abundance of *R. nubila* and chironomid larvae is somewhat surprising since they also are consumed by *H. siltalai*, but apparently hydropsychid nets enhanced food availability to these taxa, and so the presence of *H. siltalai* resulted in a positive facilitation.

Strong competitive interactions involving stream macroinvertebrates have been demonstrated with sessile or slow-moving grazers, due to a combination of exploitation and interference competition. Snails of the family Pleuroceridae appear to be competitive dominants in those headwater streams where they reach high abundances. Both *Juga silicula* in the northwestern US and *Elimia clavaeformis* in the southeast have been reported to reach high densities and to make up more than 90% of the invertebrate biomass (Hawkins and Furnish 1987; Hill 1992). Snails can graze periphyton to very low levels, and because of their large size, individual snails also may harm other species by "bulldozing" over substrate surfaces. The interaction between *Elimia clavaeformis* and the caddis *Neophylax etnieri* in a headwater stream in Tennessee makes a strong case that the snails' influence is via exploitative competition (Hill 1992). High dietary overlap determined from gut analysis suggested that these two grazers were competing for periphyton. Both species substantially increased their growth rates and condition (ash free dry mass per unit wet mass) when transferred from the stream to a high quality diet in the laboratory, suggesting food limitation in nature. In a natural experiment, Hill examined periphyton abundance and *Neophylax* condition in six streams lacking *Elimia*, and in six streams where the snail was abundant. Periphyton biomass was three times greater and caddis larvae at diapause roughly twice as large in the absence of snails (Fig. 10.18).

Manipulation of a large herbivorous snail (*Sulcospira hainanensis*) in Hong Kong streams demonstrated a competitive effect on grazing insects, due to reduction of algal abundance by grazing snails, but only during the dry season (Yeung and Dudgeon 2013). During the dry season, algal biomass was greater and mayfly densities markedly higher on tiles where wire mesh barriers reduced snail densities by about 30–50% relative to controls (Fig. 10.19). Differences were minor during the wet season, when spate-induced disturbance overrode the biotic interaction. This is in agreement with predictions of the harsh-benign hypothesis, which asserts that biotic interactions are most important under relatively benign environmental conditions—often low and constant flows—and less so under unfavorable conditions such as frequent scouring flows.

Armored grazers, including snails, stone-cased caddisfly larvae, and neotropical armored catfishes, whose protection from predators provides an advantage over less defended grazers such as mayflies, can become very abundant and are capable of reducing algal levels sufficiently that other grazers are disadvantaged. The caddis larva *Glossosoma* has been shown to be an effective grazer of periphyton and competitor with other macroinvertebrates in several studies. Its slow rate of movement and efficient grazing reduce periphyton to low levels, allowing it to maintain high population densities at relatively low resource levels, and its stone case deters predation. By erecting barriers of petroleum jelly in a Montana stream, McAuliffe (1984a, b) was able to achieve approximately a fivefold reduction in *Glossosoma* densities, which resulted in a twofold increase in algal cell density. Mobile grazers such as *Baetis* were significantly more abundant in areas where *Glossosoma* was excluded. At normal densities *Glossosoma* appears able to reduce algal densities to levels where *Baetis* experiences resource limitation, and thus exploitation rather than interference is the primary mechanism. A 10-month exclusion experiment in a Michigan springbrook of very constant flow provides additional evidence of the community-wide effects of *Glossosoma*. Periphyton biomass increased substantially, as did the densities of most grazers (Kohler 1992). Following a 60-day experiment in a headwater stream in northern California, US, in which *G. penitum* was removed from 4-m^2 stream sections, reducing its biomass by 80–90%, chlorophyll a

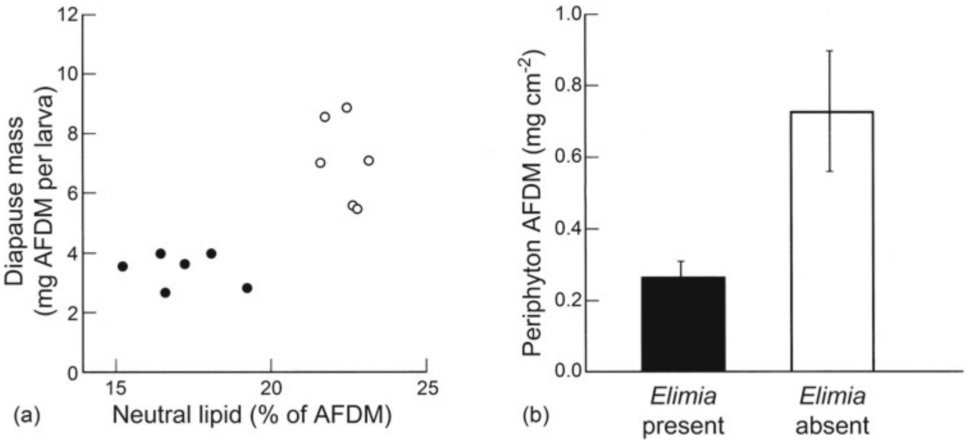

Fig. 10.18 Comparison of six streams in the southwestern US lacking the snail *Elimia clavaeformis* versus six streams where the snail was extremely abundant. (**a**) Average mass of diapausing larvae of the caddis *Neophylax* were higher in the absence of snails. (**b**) Periphyton mass also was higher in the absence of snails (Reproduced from Hill 1992)

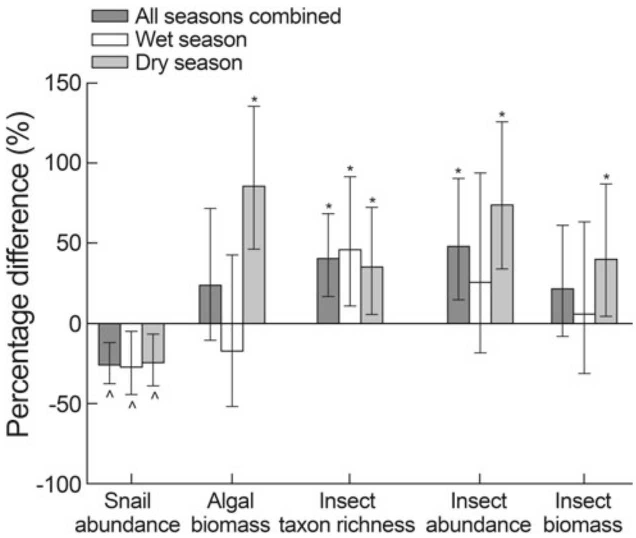

Fig. 10.19 Experimental reduction of an abundant grazer, the snail *Sulcospira hainanensis*, resulted in much more algal biomass, and greater abundance and biomass of grazing insects in Hong Kong streams, but effects were strong only in the dry season. Spate-induced disturbance during the wet season appeared to override this biotic interaction, an example of what is often referred to as the harsh-benign hypothesis. Values shown are mean percentage difference and associated 95% confidence intervals (Reproduced from Yeung and Dudgeon 2013)

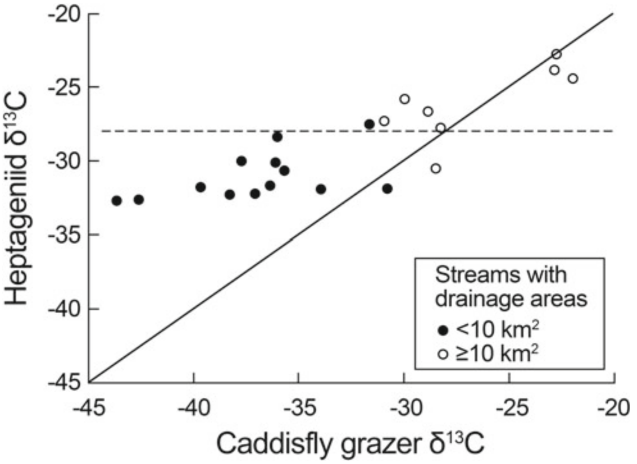

Fig. 10.20 Stable carbon isotope ratios of heptageniid mayfly larvae (*Cinygma*, *Cinygmula*, *Nixe*, and *Epeorus*) from the South Fork Eel River watershed (California, US) plotted against those of grazing caddisflies (*Glossosoma penitum*, *Glossosoma califica*, and *Neophylax rickeri*). Each point represents isotope ratios of caddisflies and mayflies collected from the same stream and habitat on the same date. Streams range from drainage areas of 0.8–145 km^2. Algal ^{13}C values generally increase with stream size in the watershed (Finlay 2004); the most ^{13}C-depleted values correspond to the smallest and least productive streams. Solid circles represent streams with drainage areas < 10 km^2. In small unproductive streams, mayflies' carbon isotope ratios are intermediate between those of detritus (dotted line) and scraping caddisflies. As stream size increases, the stable carbon isotope ratios of mayflies and caddisflies converge (Reproduced from McNeeley et al. 2007)

increased twofold and algal consumption by heptageniid mayfly larvae increased as well (McNeeley et al. 2007). While this result supports the view that mayflies experienced competitive release due to an increased food supply, less algal carbon passed through mayfly grazers than expected, possibly because scraping caddisflies consume primarily algae whereas mayfly diets include algae and detrital carbon in variable proportions. Indeed, comparison of stable carbon isotope ratios of caddis and mayfly larvae from multiple stream sites suggests that their diets converge at larger and more productive sites where algae are more abundant and comprise the primary diet of mayflies (Fig. 10.20). This provides yet another example that environmental context can determine whether competition has noticeable effects.

Collectively, these studies demonstrate that competitive interactions indeed take place among macroinvertebrate assemblages of streams, but the extent and magnitude of competitive effects in natural systems are not well resolved. However, observations that accompanied the collapse of *Glossosoma nigrior* populations in Michigan trout streams due to outbreaks of the microsporidian *Cougourdella* provide impressive documentation of the ecosystem-wide influence of a dominant grazer (Kohler and Wiley 1997). The pathogen-induced decline of *Glossosoma* resulted in marked increases in the biomass of periphyton (Fig. 10.21) and in the abundance of most grazers and filter-feeders (Fig. 10.22). Remarkably, these changes dovetailed with results from Kohler's (1992) prior laboratory and field experiments in a stable, spring-fed stream where *Glossosoma* was the dominant grazer. Long-term exclusion of *Glossosoma* resulted in increases in periphyton biomass and in the abundance and growth of a number of other species of grazers including midge larvae, indicating that the caddis larva might influence other members of the assemblage through diffuse competition. Two sessile filter-feeders, the black fly *Simulium* and the midge *Rheotanytarsus* also increased in the *Glossosoma* exclusion, which may reflect interference competition from physical encounters with the more robust *Glossosoma*. Inspection of Fig. 10.22 leaves little doubt that, in this system, competition from a dominant grazer has dramatic, system-wide consequences. It also is instructive that although all responses were in accord with results from previous, smaller-scale experiments, those studies underestimated the extent and magnitude of *Glossosoma*'s influence.

Finally, as several examples show, environmental factors influence the outcome of competitive interactions. Resource suppression by a dominant grazer resulting in indirect competitive effects on grazing insects was limited to the dry season (Fig. 10.19, Yeung and Dudgeon 2013) when conditions were relatively benign. Invasion success and extent

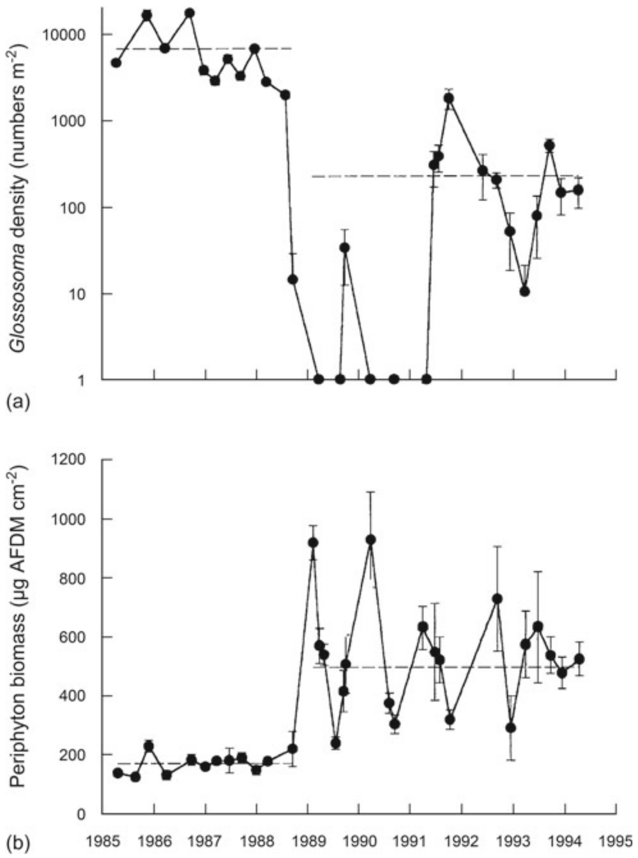

Fig. 10.21 Density of *Glossosma nigrior* (**a**) and biomass of periphyton (**b**) in Spring Brook, Michigan. Horizontal dashed lines are the overall mean density or biomass for the periods before and after *Glossosoma's* collapse in 1988. Values are means +1 SE (Reproduced from Kohler and Wiley 1997)

of spatial overlap between competitively dominant non-natives and native species depends on both temperature and hydrologic regime (Fausch et al. 2001; McHugh and Budy 2005). For all of the above reasons, it is likely that the influence of competition within stream communities will vary among locations, over seasons, and between different species assemblages.

10.4 Parasitism

Organisms that infect or parasitize their hosts typically result in the reduced health and fitness of the host, and sometimes parasitism results in death. Microparasites, also called pathogens, are small organisms capable of multiplying within a host, including viruses, bacteria, fungi, and protists. Macroparasites typically are larger and do not multiply directly within individual hosts; this includes flatworms (trematodes), roundworms (nematodes), tapeworms (cestodes), spinyheaded worms (acanthocephalans) and ectoparasitic arthropods (ticks, copepods, mites, and water lice) (Johnson and Paull 2011). Parasites can infect a single host; however, some pass through one or more intermediate hosts before reaching their definitive (terminal) host.

Parasites can have profound effects on the behavior and abundance of their hosts, including ripple effects that affect other species that interact with the host. The immediate effects of a pathogen on its host include reduced growth, increased susceptibility to predators, and reduced fitness. Beyond these effects on individuals, pathogens can profoundly influence host population dynamics, and when a susceptible species encounters a virulent, often novel pathogen, the results can be catastrophic. Pathogen populations typically are assessed based on their prevalence (the proportion of the host population that is infected), and abundance (also called intensity, the number of individual pathogens per infected host) (Bush et al. 1997). In a host-pathogen interaction where long exposure presumably has allowed the host to adapt to infection, host and parasite abundance may remain relatively stable. However, just as a new infection can sweep through a human population, the arrival of a novel pathogen can result in such a rapid decline of its host that its populations virtually disappear.

Parasites and pathogens potentially may also produce effects that spread indirectly to other members of the community. By influencing host abundance, they may have top-down effects similar to strongly interacting predators and grazers. In addition, parasites and pathogens can influence host traits including behavior and morphology, thus having trait-mediated indirect effects on other species. When the host species is itself a strong interactor with other members of the food web, the effects of its decline can ramify widely.

Freshwater ecosystems harbor pathogens and parasites responsible for a number of well-known animal diseases including salmonid whirling disease, amphibian chytridiomycosis, and crayfish plague. Diseases affecting human populations, such as malaria, cholera, and river blindness, among others, are also linked to fresh waters (Johnson and Paull 2011). Fishes are affected by many types of pathogens including viruses causing anemia and kidney failure, myxozoans causing whirling disease and proliferative kidney disease, as well as by bacteria, fungi, helminths, protists, and arthropod parasites. In contrast, host-pathogen interactions among aquatic insects have received little study, and the majority of research has focused on the effects on host fitness, with only a small number of studies examining population or community-level effects (Kohler 2008). In all likelihood, the influence of pathogens on aquatic invertebrates is under-appreciated. From DNA extraction of 10 species of aquatic insect larvae and two amphipods of the genus *Gammarus* from a low mountain stream in Germany, a total of 26 parasite species, including 12 microsporidians and 10 helminths, were detected in 12 host species, most

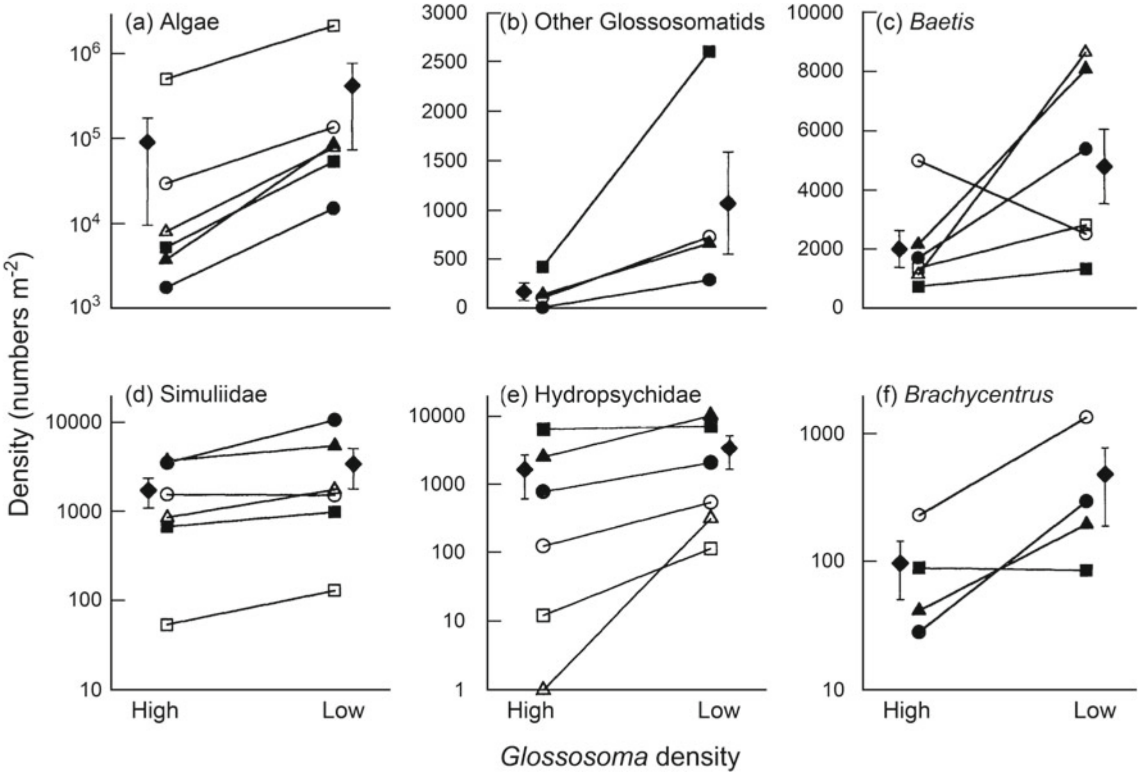

Fig. 10.22 Mean abundances of periphyton (as algal cells cm^{-2}) (**a**), periphyton-grazing insects (**b–c**), and filter-feeders (**d–f**) as a function of *Glossosoma* density (high, low = prior to or during recurrent pathogen outbreaks, respectively) in six streams from southwest and northern lower Michigan. Invertebrate densities are expressed as number of individuals m^{-2}. Symbols denote the six streams (Reproduced from Kohler and Wiley 1997)

with surprisingly high prevalence (Grabner 2017). Microsporidians were present in all host species, and trematodes were present in all but one caddis larva. Nematodes were detected in five host species, and three acanthocephalan species were detected in the amphipods. However, specific host-parasite associations were relatively rare.

Nematodes in the family Mermithidae are frequent internal parasites of mayflies. Infections often are visible as coiled juveniles within the abdomen of hosts, and have been reported in Ephemeroptera, Plecoptera, Trichoptera, and Diptera. In high elevation streams of the Rocky Mountains, US, the number of individuals of larval mayflies infected by the genus *Gasteromermis* varied widely, but was estimated at 22% of the summer generation of the genus *Baetis* (Vance and Peckarsky 1996). Half of the infected larvae were estimated to die before emerging as adults, and because mermithids castrate their hosts, even those that survive to adulthood fail to reproduce, indicating that parasitism can be an important source of population mortality. However, parasites may be overlooked for a variety of reasons. While mermithids often are readily seen through the integument of a larval insect, this may not always be the case. Lancaster and Bovill (2017) observed well-developed parasitic juvenile worms in the abdominal cavities of six species of the caddis *Ecnomus* from a stream of central Victoria, Australia, but only in adults, not in larvae. Presumably the infection occurred during the larval stage, and the parasite underwent rapid growth during or shortly after pupation.

Some diseases that have been known for many decades have re-emerged in recent years, and others that have only recently emerged are becoming widespread. Emerging infectious diseases are those that appear for the first time in a population, or suddenly increase in incidence or geographic range (Daszak et al. 2000). The basis for disease emergence can be difficult to determine, as it may involve newly identified species or newly evolved pathogen traits interacting with human-induced environmental change, species invasions, and evolutionary adaptations by pathogen and host. Some dramatic examples are discussed below, each of which meets the definition of an emerging disease.

Amphibian populations have declined dramatically and globally in recent decades, mostly since 1980 (Lips et al. 2006). While a number of causal factors have been implicated and some declines are enigmatic, a virulent fungal pathogen of amphibians, *Batrachochytrium dendrobatidis*, is thought to be responsible in many instances (Collins and Storfer 2003). First described in the late 1990s, Chytridiomycosis or "chytrid" is now known from six continents.

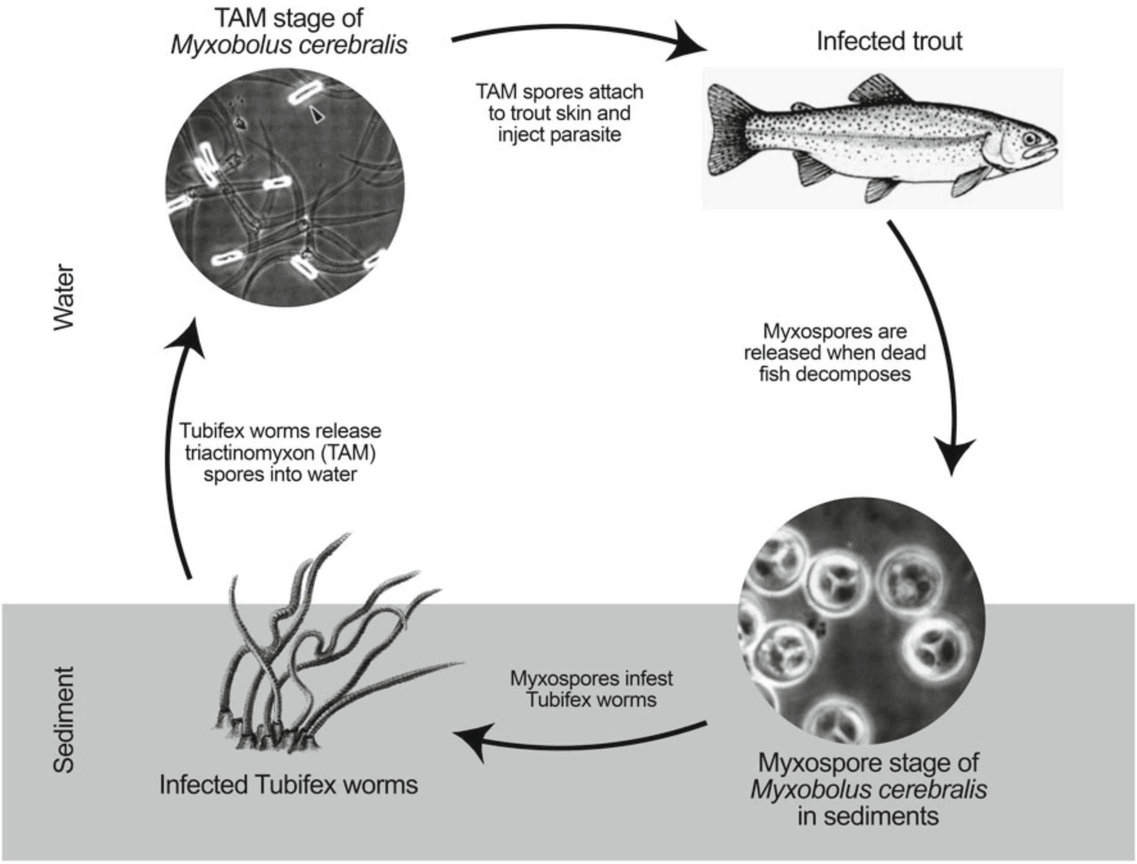

Fig. 10.23 Life cycle of *Myxobolus cerebralis*, the agent of whirling disease

A cutaneous fungal infection that manifests only in amphibians, its free-living zoospore stage infects the skin, causing some species to die within weeks, while others are little affected. Mortality apparently is due to disrupted epidermal function and osmotic imbalance. The only known host is larval and adult amphibians, and chytrid is thought to be amongst the greatest wildlife epizootic events ever documented, causing a wave of species loss in the New World tropics. Many affected species are stream-associated frogs at medium to high altitude, in protected forested sites in the tropics of Central and South America and northern Australia (Skerratt et al. 2007). North American species also have been severely impacted, including the mountain yellow-legged frog (a species complex consisting *of Rana muscosa* and *Rana sierrae*) in California's Sierra Nevada mountains (Vredenburg et al. 2010).

Myxobolus cerebralis, a myxozoan fish pathogen known as whirling disease, was first detected in 1893 in Europe, in non-native rainbow trout, but is suspected of originating in brown trout in Eurasia (Bartholomew and Reno 2002; Sarker et al. 2015). It spread worldwide with the cultivation of salmonids in fish hatcheries, appearing in wild populations in the western US after the 1980s. *Myxobolus cerebralis* has a complex, 2-host life cycle alternating between salmonid fish and the oligochaete *Tubifex tubifex*, producing waterborne spores within each host (Fig. 10.23). The only species of aquatic oligochaete known to be a suitable host, *T. tubifex* is a cosmopolitan and hardy species able to survive drought and food shortages by secreting a protective cyst and lowering its metabolic rate. Spores attach to mucous cells of the trout's epidermis, the gill respiratory epithelium, and the buccal cavity, penetrating epidermal tissues and migrating along nervous tissue to cartilage. Common symptoms are skeletal deformities and tail-chasing swimming behavior that gives this disease its name. The parasite produces myxospores inside infected fish that are released into the sediment upon death of the fish, and then ingested by tubifex worms. Species of salmonids differ in susceptibility, as rainbow and cutthroat trout are rated as highly susceptible, whereas brown trout are resistant and only develop the disease when exposed to very high parasite doses. Whirling disease has been effectively managed in hatchery-reared salmonids by rearing young fish in well water to prevent or reduce exposure of young susceptible fish, and also by chemical treatment and exposure to UV radiation. Initially thought to be primarily a problem within hatcheries, whirling disease has since been implicated in the decline of wild cutthroat trout populations in the western US. Greatest infection risk appears to be associated with habitat and temperature conditions that favor *T. tubifex* and spore production, and co-occurrence with diseased trout, particularly rainbow trout, which are both highly susceptible and widely stocked (Ayre et al. 2014).

The fungus-like organism *Aphanomyces astaci* (Oomycetes) causes crayfish plague, growing in melanized areas of the cuticle and spreading by asexual swimming zoospores. North American crayfish species are largely immune, apparently as a result of having evolved with the parasite, but the disease is devastating to European crayfishes, causing stress to the immune system and rapid death (Holdich et al. 2009). First introduced into Europe in the mid-nineteenth century, the late 20th century arrival of several, highly invasive North American crayfish species that are natural hosts has led to further spread of the disease and declines in European species. Availability of migration routes and suitable habitat for invasive crayfish species will determine geographic spread. However, some argue that *Aphanomyces astaci* may be over-diagnosed as the causative agent of die-offs in crayfish, at least until the recent, wider use of molecular identification methods. Other pathogens may have been undetected as crayfish harbor a number of disease-causing agents including viruses, bacteria, fungi, protists and metazoans (Longshaw 2011; Edgerton et al. 2019). Although generally considered a pathogen specific to crayfish, other freshwater decapods may be vulnerable as well (Svoboda et al. 2014).

Invasive species may be important hosts and vectors of pathogens brought to a new region where, much as introduced predators can devastate naïve prey, novel pathogens can quickly cause epizootics (i.e., outbreaks of infectious diseases in non-human animals) (Poulin et al. 2011). The introduction of crayfish plague from North America to Europe is one example, and the spread of whirling disease and its subsequent transfer from hatchery-reared trout to wild trout is another. When a pathogen is of high virulence to a native species but low virulence to an invading species, ‘spill-over’ of the parasite can cause high mortality to the native species, or reduce its ability to compete with the invader. This is sometimes referred to as parasite-mediated competition, and is likely to be most severe when the invading species is sufficiently abundant to cause high exposure of the native species to the pathogen. The timeline of the decline of the noble crayfish (*Astacus astacus*) in Sweden due to crayfish plague illustrates this well (Bohman et al. 2006). Due to declines of noble crayfish following first arrival of plague in the early 1900s, and market demand for freshwater crayfish, beginning in 1969 the government began a large-scale introduction of the American signal crayfish (*Pacifastacus leniusculus*), a chronic carrier of *Aphanomyces astaci*. Comparison of the number of outbreaks for the 20-year period before (1940–1960) and after (1975–1995) shows the further geographic spread of crayfish plague with time, and the increased frequency of disease outbreaks following the widespread cultivation of signal crayfish (Fig. 10.24). In addition, once introduced, a pathogen may take up residence in native species, and its further spread may be independent of the original host species. The intestinal nematode *Camallanus cotti* is thought to have invaded Hawaii via the introduction of poeciliid fishes used in mosquito control, and now infects native Hawaiian fishes including the goby *Awaous stamineus*. Surveys by Gagne et al. (2015) show that the parasite has become decoupled from its original host, as it has spread beyond the range of its introduced host to streams that have no record of poeciliid presence, although the mechanism of its dispersal is not yet established.

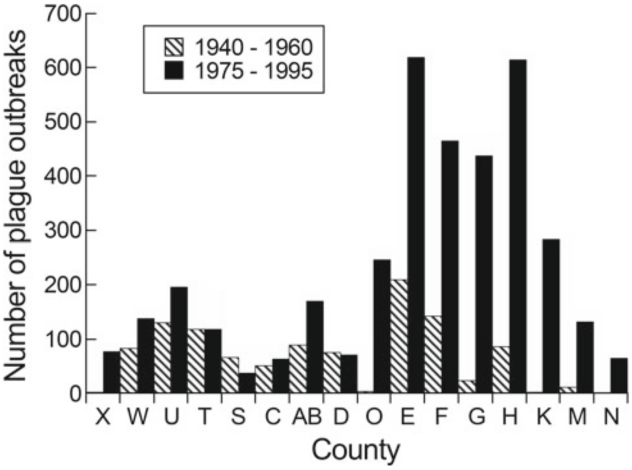

Fig. 10.24 A comparison of crayfish plague outbreaks for each county in Sweden occurred during two periods, before (1940–60) and after (1975–94) the introduction of the signal crayfish in Sweden. The counties are arranged from north to south (letters X to M). Only counties that have reported crayfish outbreaks are represented in the chart (Reproduced from Bohman et al. 2006)

One final example of parasitism in stream-dwelling organisms deserves mention, that involving the larval stage of certain mussels, because it is so fascinating and unique. Unionid mussels have a larval stage that is temporarily parasitic on fish. The benefit to mussels is dispersal, including upstream transport, and the energetic cost to the fish of an immune response generally is low. The variety of ways that glochidia are released, their attachment mechanisms, and in some mussels the ability to attract fish hosts by mimicking prey, make fascinating natural history (Barnhart et al. 2008). Mature glochidia are expelled individually, in loosely bound mucous masses, or bound together in discrete packages by a mucoid or gelatinous matrix, and can be distinguished by the number and shape of attachment hooks. Some aggregates have the appearance of prey and are ingested by fish, settling in the gills. Several species of Lampsilinae have evolved mantle margins that undulate to

Fig. 10.25 A greenfin darter (*Etheostoma chlorobranchium*) freshly captured by a female Oyster Mussel (*Epioblasma capsaeformis*). The mussel will release her parasitic larvae to attach onto fins and soft tissues, and then release the fish to disperse these larvae. Clinch River, Tennessee. Photo by David Herasimtshschuk, Freshwaters Illustrated

attract fish seeking prey, and the genus *Epioblasma* captures its fish host in its valves to facilitate transfer of glochidia (Fig. 10.25). After a brooding time that varies among taxa, larvae detach and fall to the substrate, taking on the typical form of a juvenile mussel. Mussels show varying degrees of host specificity from use of a single host species to many, since as temporary parasites, mussels must circumvent the immune responses of the host to complete this life stage. However, the preferred hosts are known for only some of the 300 or so species of North American Unionidae.

10.4.1 Direct and Indirect Effects

The most obvious direct effect of a pathogen on its host is a reduction in growth and reproductive fitness, or simply death of the host. Changes in the morphology or behavior of an infected host also may occur, possibly as an adaptation that benefits either host or parasite, depending on which of the two appears to gain some advantage. Changes in host behavior as a consequence of parasitism could be simply a pathological side effect of parasite infection, such as reduced mobility, a host-adaptive strategy such as behavioral fevers, or a parasite-adaptive strategy, such as making a secondary host more vulnerable to predation by a definitive (terminal) host. Seeking warm water when infected has been documented in a number of fish species, including the Trinidadian guppy *Poecilia reticulata* when infected with a common helminth ectoparasite that feeds on skin and fin tissue. Infected guppies showed a preference for temperatures above 30 °C, which are known to impede trematode growth (Mohammed et al. 2016).

In two-host systems where it benefits the parasite to induce the intermediate host to ‘commit suicide” so as to reach its definitive host, some impressive examples of behavior modification have been documented. The life cycle of parasitic hairworms (Nematomorpha: Gordiida) requires two critical transitions across habitats, first from aquatic hosts such as insect larvae to terrestrial definitive hosts (crickets and grasshoppers) and second from the definitive hosts back to water (Schmidt-Rhaesa and Ehrmann 2001). In a well-known example of parasite manipulation of host behavior, crickets infected by mature hairworms seek and jump into water, at which time adult worms emerge and free-living individuals begin searching for sexual partners. The crickets, now wriggling at the water surface, constitute a terrestrial prey subsidy to fish (Ponton et al. 2006; Sato et al. 2008). Amphipods in the genus *Gammarus* can be infected with the acanthocephalan parasite *Pomphorhynchus laevis*, which completes its life cycle when the amphipod is eaten by a fish predator capable of serving as definitive host. In the River Teme, England, approximately 20% of adult *G. pulex* were infected with *P. laevis*, and the drift of parasitized amphipods was significantly greater than that of unparasitized individuals (McCahon et al. 1991). Because the acanthocephalan must complete its development in the gut of a trout or other drift-feeding fish, altering amphipod behavior to make it more likely to drift is clearly to the parasite’s advantage.

Mermithid nematodes also have been reported to alter host behavior. Infected nymphs of mayflies in the genus *Baetis* were consumed significantly more by a predaceous stonefly than unparasitized nymphs, apparently because they were less prone to escape the approaching predator

(Peckarsky and Vance 1997). Similarly, mermithid-infected nymphs of mayflies in the genus *Deleatidium* were disproportionately represented in drift samples compared with benthic samples, suggesting that infection by mermithids results in an increased tendency to drift, where they would be more susceptible to fish predation (Williams et al. 2019). However, in neither case is there an apparent advantage to the parasite, which usually emerges when the adult mayfly enters the water to lay its eggs. These two studies of the increased susceptibility of infected mayfly hosts to predation suggest a third possibility, namely that the change in behavior is a non-adaptive, pathological side effect of infection. In neither case is there an advantage to the parasite, such as transference to a final host, as the insect is the only host to the nematode; in addition, the life cycle of most common mermithids found in stream insects is completed when adult mayflies enter the water to oviposit on substrates. Thus, the most apparent effect of mermithid parasitism is to harm host reproductive fitness, and it is in the parasite's interests that its host not be eaten during its larval life.

Interestingly, the mermithid *Gasteromermis* does alter the behavior of adult *Baetis* males (Vance 1996). In uninfected individuals, adult females crawl down the side of a rock into the water to oviposit, but males of course do not. When an infected female enters the water, the mermithid escapes through a puncture wound in the mayfly's abdomen. Infected males are feminized, meaning they behave like females, with the same ovipositing behavior that favors mermithid escape. Further illustrating the complexity of host-parasite interactions, the mermithid *Pheromermis* requires two hosts: an aquatic insect as an intermediate aquatic host and a terrestrial definitive host, vespid wasps, which acquire the infection by consuming the adult of the aquatic insect (Poinar 1976). Surveys of the Guare and Emilia rivers in northern Venezuela found *Pheromermis* juveniles coiled inside stonefly nymphs collected at multiple sites (Gamboa et al. 2012). Prevalence was over 90% in both in *Anacroneuria blanca* and *A. caraca*, indicating that larvae of this stonefly to be important hosts of this mermithid in these rivers. However, the terminal host remains unknown.

When the prevalence and abundance of a pathogen is great enough, it may regulate its host's population or, in extreme cases, drive it to extinction as appears to be the case with chytrid and some anurans. A 15-year monitoring study of a caddisfly (*Brachycentrus americanus*) and the prevalence of a microsporidian disease provided convincing evidence that the disease was largely responsible for driving observed *Brachycentrus* population dynamics in a stream in Michigan, US (Kohler and Holland 2001). Both the host and its pathogen exhibited cyclical dynamics with a lag of one generation, evidence of delayed density-dependent parasitism as disease prevalence tracked increases and declines in the caddis population. The caddisfly *Glossosoma nigrior* occurs with the microsporidian *Cougourdella* at some locations but not others, causing strikingly different *Glossosoma* dynamics depending on the presence of the microsporidian (Kohler 1992). *Glossosoma* populations did not fluctuate greatly in the absence of *Cougourdella*. In contrast, where *Cougourdella* infections had been detected, *Glossosoma* populations existed either at high densities where *Cougourdella* prevalence was consistently low, or at low densities due to recurrent *Cougourdella* epizootics. *Glossosoma* is a particularly strong interactor capable of reducing attached algae to very low levels and relatively invulnerable to predators due to its case of small stones (Kohler and Wiley 1997). As described earlier, since this system provided strong evidence of competition, pathogen-induced reductions in *Glossosoma* abundance resulted in increased abundance of attached algae (Fig. 10.21), and population sizes of most other algal consumers increased, evidence of competitive dominance by the caddis larva and the indirect benefit to other grazers resulting from *Cougourdella* outbreaks (Fig. 10.22). As further evidence of the community-wide influence of this pathogen-host interaction, invertebrate predators doubled in abundance following *Glossosoma* population collapse.

Because the tadpoles of many species of amphibian feed on algae and detritus, and chytrid-induced declines of amphibian populations can be extreme, ripple effects throughout food webs can be substantial (Whiles et al. 2006). Manipulation of tadpole access to experimental tiles in a Panamanian stream using an electric field showed that tadpoles significantly reduced organic particles and diatom abundance and diversity, while tadpole exclusion enhanced abundance of grazing mayflies (Ranvestel et al. 2004). The dramatic decline in amphibian tadpole populations driven by a chytrid outbreak had profound, ecosystem-level consequences in a relatively undisturbed wet-forest stream in Panama (Whiles et al. 2013). Tadpole biomass in 2008 was 2% of the value in 2006, resulting in a doubling of algal and fine detrital biomass. The uptake and cycling of nitrogen, measured with a tracer addition of ^{15}N, was markedly lower, apparently because of changes to mineralization rates (less ingestion and excretion by tadpoles) and lower export of fine particulates (reduced bioturbation). Surprisingly, unlike the study of Kohler and Wiley (1997), other grazers did not increase, indicating that other grazers were not able to compensate for the loss of tadpoles.

10.5 Summary

Species are interconnected through the proximate food chain linkages of herbivory, predation, competition, and parasitism. The supply of resources is potentially limiting to consumers, and an abundance of consumers may in turn deplete resource levels. The importance of these bottom-up and top-down effects is seen in foraging and risk-avoidance adaptations, in the size of populations, and through indirect effects on species several steps removed from the initial interaction. Consumers of the same resource are competitors whenever resource sharing is mutually detrimental, but various mechanisms of resource partitioning may sufficiently reduce overlap to permit coexistence. Parasites and pathogens can reduce host growth and fitness, alter host behavior, and in some cases cause direct mortality. The strength of species interactions is most evident when the abiotic environment is moderate, and may be reduced or undetected whenever environmental variation is extreme.

The study of herbivory in stream ecosystems has focused mainly on the grazing of benthic algae by invertebrates, some fishes, and a few amphibian species. Benthic algae vary in their distribution, growth form, and nutritional value, and grazers differ in their means of scraping and browsing this food supply. Grazers have numerous impacts on algae, reducing their abundance, altering assemblage composition, and even stimulating algal growth and overall productivity through the removal of senescent cells and the recycling of nutrients. Studies comparing the balance of carbon, phosphorus, and nitrogen between herbivores and their food resources provide insight into the nutritional quality of periphyton to herbivores, and the role of consumer egestion and excretion in recycling nutrients to the benefit of primary producers. Strong effects of herbivory in streams have been documented with a number of invertebrates, including snails and some caddisfly and mayfly larvae, and in fishes such as the stoneroller in North America and armored catfishes in the Neotropics. Under the usually moderate environments in which most grazing studies are carried out, top-down control of algae by grazing appears to be at least as strong as bottom-up control by nutrient supply. Disturbance, particularly due to extremes of flow, can alter the grazer-algal dynamic by reducing grazer abundance, and heavy grazing pressure can reduce algal biomass to a level where it is less vulnerable to scouring during high flows.

Predation affects all organisms at some stage of the life cycle, and many species encounter predation risk throughout their lives. It affects individuals and populations directly through consumption and mortality, and also can result in behavioral and morphological adaptations that may entail some fitness cost to the prey. The many fascinating examples of the foraging behavior of predators and risk-avoidance tactics of prey attest to the importance of this interaction to both parties. Prey species depart from risky environments, restrict the time of day and location of foraging, and evolve defensive morphologies that may exact a cost in growth or subsequent reproduction. Because the prey are themselves consumers of other resources, these responses help us to understand how the indirect effects of top predators can extend throughout the food web. Top predators have often but not invariably been demonstrated to limit the abundance of prey populations, to confine the prey's distribution to habitats where the predator is absent or ineffective, and in some instances to trigger an elaborate cascade of interactions with consequences for whole ecosystems. Habitat conditions, the identity of the top predator, the magnitude of external subsidies, and environmental disturbance can act as switches that turn a cascade into a trickle, or the reverse.

Competition between consumers for a shared resource either through its mutual exploitation or by aggressive interference depends on the extent of niche overlap versus niche segregation. Estimates of overlap in diet, habitat, or temporal activity of groups of species that share a common resource are often used to infer competition. Field observations such as the different mesh sizes and locations of the nets of hydropsychid caddis larvae or use of stream habitat and time of day for foraging by stream fishes suggest how interactions within groups of potentially competing species can be ameliorated through the partitioning of diet, space, or time. The large literature on resource partitioning among stream-dwelling invertebrates and fishes provides much insight into the specialization of individual species, but because the extent to which resources actually are limiting often is unknown, this is weak evidence for the importance of competition. Experimental studies with invertebrates have documented numerous cases of aggressive interference, mainly involving space limitation, and in some cases the interaction is as much predation as competition. Evidence to date may reflect challenges of experimental design and scale, as is suggested by the system-wide effects that followed the decline of an abundant grazing caddis affected by a parasite outbreak. It seems that competition can be an important interaction in stream assemblages, but the extent of its influence is not well understood.

Freshwater ecosystems harbor pathogens and parasites responsible for a number of well-known animal diseases including salmonid whirling disease, amphibian chytridiomycosis, and crayfish plague, as well as diseases affecting humans, such as malaria, cholera, and river blindness. Some infect a single host, while others pass through one or more intermediate hosts before reaching their definitive (terminal) host. In the latter case, parasites may alter host behavior, making it more vulnerable to consumption by the definitive host. Host-parasite relationships involving fishes have received considerable study, relative to those involving aquatic invertebrates. Where long exposure presumably has allowed the host to adapt to infection, host and parasite abundance may remain relatively stable. However, the arrival of a novel pathogen can result in such a rapid decline that the host population virtually disappears, as evidenced by many species of neotropical amphibians infected by a virulent fungal pathogen. Severe infections may arise when brought to a new region by an invasive species that hosts but is relatively resistant to the parasite or pathogen, or when some change to environmental conditions favor its emergence.

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